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Introduction to the International Symposium on the Biological Characteristics of Herring and Their Implication for Management

F. H. C. Taylor

Pacific Biological Station, Nanaimo, B.C. V9R 5K6

To celebrate its 75th anniversay the Pacific Biological Station (Fisheries Research Branch, Department of Fisheries and Oceans) sponsored the International Symposium on the Biological Characteristics of Herring and Their Implication for Management, held in Nanaimo, British Columbia, from June 20 to 22, 1983.

The Pacific Biological Station was founded in 1908 under the direction of Rev. G. W. Taylor, a naturalist and member of the Royal Society of Canada. Until 1924 the station depended on volunteer investigators, mainly from universities. Research concentrated on the taxonomy, distribution, and life history of marine plants, invertebrates, and fish. A strong surge of interest in practical fisheries problems in the mid-1920s resulted in the recruitment of the first permanent staff. In the next decade, major projects initiated included an intensive study of the relative efficiency of natural and hatchery propagation of sockeye salmon, the tagging of chinook and coho salmon, and the investigation of the productivity of pink salmon in the Queen Charlotte Islands. This decade also marked the beginning of research on oysters, clams, crabs, shrimps, prawns, and marine borers and on the physical and chemical oceanography of British Columbia waters.

Research on herring, at first in conjunction with pilchards, which were abundant at that time, began in 1929 although the commercial fishery for herring dated back to 1877. Annual catches remained below 600 tonnes (t) until 1902, and then climbed to 9000 t by 1907. In response to the development of an oriental market for dry-salted herring, catch levels rose to about 25 000 t by 1919, to 78 000 t by 1927, and then fell to 26 000 t in 1934 with the decline of this market. The introduction of a meal and oil reduction fishery for pilchards and herring in 1935 lead to a dramatic expansion of the fishery and to the initiation of a major herring research program, which has continued with some shift of emphasis ever since. Increase in the reduction fishery lead to the doubling of herring catches in 1936 and 1937. Catches then averaged close to 100 000 t to 1946, jumped to 156 000 t in 1947, and then averaged about 190 000 t until 1965 (omitting 1953 and 1958 when catches were held down by industrial disputes).

After the early 1940s, when the contribution of pilchards became insignificant, herring stocks bore the full pressure of the ever-increasing reduction fishery until these stocks collapsed in the late 1960s. By this time herring stocks on all parts of the coast had been fully utilized. All fishing was curtailed. Following the recovery of the stocks in the early 1970s, there emerged a fishery for roe herring for sale to Japan. Since 1972 catches have averaged about 40 000 t per year, and have been maintained at this conservative level to the present time.

Up to the end of the reduction fishery in the 1960s, fishing was conducted almost entirely by purse seine. Gill nets were subsequently introduced in the roe fishery. Their share of the catch increased from 2% in 1972 to roughly 50% in recent years.

In addition to the roe fishery a food export fishery began in 1976, and has accounted for about 20 000 t annually since 1978. Also, local food and bait fisheries have continued to take 5000 t, mainly from stocks not appreciably exploited by the roe fishery. Concurrently with the roe fishery a small but lucrative "spawn-on-kelp" fishery has developed. Since the development of the roe fishery, herring have ranked second in landed value to the sum of all species of salmon, and exceeded in value any single species.

Herring was selected as the subject of this symposium both because of its importance in the fisheries economy of British Columbia and because of difficulties worldwide in managing its fisheries. Other herring fisheries have also undergone similar large fluctuations. The symposium, consisting of five sessions of invited and contributed papers, provided a forum to examine problems of (1) herring biology in relation to management, (2) the ecological requirements of the various life history stages and stocks, and the major factors affecting them, (3) the response of stocks to exploitation, (4) the success or failure of current exploitation strategies used on stocks in different parts of the world, and (5) alternate strategies to provide optimum yield under various biological, economic, and social conditions.

The Program Committee, which organised the symposium, consisted of the Chairman, F. H. C. Taylor, the Special Editor, J. R. Brett, and the Chairmen of the Sessions, D. F. Alderdice, D. E. Hay, M. Stocker, B. M. Leaman, and D. M. Ware, all on staff at the Pacific Biological Station. The committee also included R. D. Humphreys, now with the Field Services Branch, Department of Fisheries and Oceans, New Westminster, R. Deriso from the International Pacific Halibut Commission, Seattle, WA, W. G. Doubleday, Resource Research Branch, DFO, Ottawa, Ont., C. C. Lindsey and N. J. Wilimovsky of the Institute of Animal Resource Ecology, University of British Columbia, Vancouver, B.C., and J. McInerney, Department of Biology, University of Victoria, Victoria, B.C. David Cushing of Lowestoft, England, was asked to review and provide an overview of the symposium.

King Herring: His Place amongst the Clupeoids[1]

P. J. P. Whitehead

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Whitehead, P. J. P. 1985. King herring: his place amongst the clupeoids. Can. J. Fish. Aquat. Sci. 42 (Suppl. 1): 3–20.

Modern taxonomy, fishery science, and biology were born in Europe. This, together with the long-standing economic importance of the herring, has given *Clupea harengus* (and its close relative *C. pallasi*) a prestige and literature that quite outshadows those of any other clupeoid species. In fact, the two species of *Clupea* contribute about 8% to world clupeoid catches, coming fourth in the 20 economically important clupeoid genera. They belong to a group, the suborder Clupeoidei, with about 80 genera and over 330 species, with a long evolutionary history reaching back to the Cretaceous. The majority of these clupeoid species live in tropical or subtropical waters, where their fisheries are extensive; in total, the clupeoids are economically the most important single fish group, contributing up to one third of all fish catches. The vast *Clupea* literature (and the research effort that it represents), at times threatening to rival that of all other species put together, suggests an imbalance. Nevertheless, it has pioneered techniques and insights that are of great application to other clupeoids and their fisheries.

La taxonomie moderne, les sciences halieutiques et la biologie sont toutes nées en Europe. Ce phénomène et le rôle économique important que joue depuis très longtemps le hareng ont fait que le renom de *Clupea harengus*, et de son proche parent *C. pallasi*, et le nombre des ouvrages connexes, dépassent largement ceux des autres espèces de clupéidés. De fait, ces deux espèces de *Clupea* forment environ 8 % des prises mondiales de clupéidés, venant au quatrième rang des 20 genres de clupéidés d'importance économique. Elles appartiennent à un groupe, le sous-ordre des Clupeoidei, dont les près de 80 genres et plus de 330 espèces ont une longue histoire évolutive prenant ses racines au crétacé. La majorité de ces espèces vivent en eaux tropicales ou subtropicales où elles font l'objet d'une pêche extensive. Les clupéidés forment le groupe de poisson le plus important du point de vue économique ; ses prises représentent le tiers de toutes les prises de poisson. Les nombreux ouvrages, sur le genre *Clupea*, et les importants travaux de recherche qu'ils représentent ont parfois failli égaler en nombre ceux de toutes les autres espèces réunies, ce qui porte à croire à un certain déséquilibre. Ces recherches ont néanmoins été à l'origine de techniques et d'approches qui ont eu des applications dans le domaine de la pêche d'autres clupéidés et d'autres espèces.

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> Honneur aux peuples de l'Europe qui ont vu dans les légions innombrables de harengs que chaque année amène auprès de leurs rivages, un don précieux de la Nature !
>
> Lacepède: *Histoire naturelle des poissons*

Lacepède (1800, 1803) recognised 27 species of clupeoid or herring-like fishes, which he placed in 5 genera (actually 19 modern species in 17 genera: Whitehead 1967, p. 156). However, he was in no doubt that *Clupea harengus* was *the* herring, and in the spirit of his mentor Buffon he lavished upon it suitably flowery phrases (Lacepède 1803, p. 429):

> Le hareng est une de ces productions naturelles dont l'emploi décide de la destinée des empires. La graine du cafeyer, la feuille du thé, les épices de la zone torride, le ver qui fille la soie, ont moins influé sur les richesses des nations, que le hareng de l'Ocean atlantique. Le luxe ou le caprice demandent les premiers: le besoin réclame le hareng.

Bloch (1782, p. 186–206), Lacepède's immediate predecessor in the line of encyclopaedic ichthyologists, was somewhat more prosaic, but nevertheless devoted 20 pages to this one species. A quarter of a century earlier, Linnaeus (1758, p. 318), master of brevity, said it all in two words: *copiosissimus piscis*.

Copiosissimus the fish, which by the twelfth century had

[1]This paper was presented at the International Symposium on the Biological Characteristics of Herring and Their Implication for Management, convened at Nanaimo, B.C., June 20–22, 1983, commemorating the 75th anniversary of the Pacific Biological Station.

become a staple in the European diet and had so established its place that when Louis VII in 1170 granted letters patent to a guild of dealers in saltwater fish they were designated *harengères*, both to distinguish them from the *poissoniers* who handled freshwater fish and as an indication of where their principal income was derived. Even with the modern vicissitudes of the herring fisheries, which led to the 1976 closure of North Sea fishing, there were still more than a million tons of Atlantic (*Clupea harengus harengus*) and Pacific herring (*Clupea harengus pallasi*) harvested in 1978, making *Clupea* fourth in the clupeoid league after *Sardinops*, *Engraulis*, and *Brevoortia*.

Copiosissimus too the literature, which reflects the number of studies, the sheer man-hours, the salaries, the equipment, the running costs of institutes and ships — the capital investment whose mainspring (if not ultimate goal) is the greater exploitation of *Clupea* as a resource. In *Dean's Bibliography* for 1968–69, for example, there were 288 references to papers on Atlantic and Pacific herring, covering their taxonomy, morphology, physiology, ethology, ecology, zoogeography, evolution, and exploitation. Merely the listing of authors and dates occupied 2 pages or about a fifth of the 11 pages devoted to all clupeoid species.

Historically, this is perhaps not surprising. Not only has the herring from earliest times been *the* commercial fish of northern waters (after stealing the crown from the cod, *Gadus morrhua*, perhaps as early as the tenth century), but it was in northern Europe that taxonomy, fishery science, and biology first took on a modern aspect. Beginning mainly in the south with the work of men such as Pierre Belon, Guillaume Rondelet, Hippolyto Salviani, Conrad Gessner, and Ulysses Aldrovandi (all born between 1507 and 1522), contributions to ichthyology tended thereafter to come from countries to the north of the Alps and mostly those where herring was exploited and from time to time "held the fate of empires." Artedi (on whom Linneaus leaned), Gronovius, Bloch, Lacepède, Cuvier, Valenciennes, and many others all lived and worked in countries with a large traditional herring fishery and in countries that, in the nineteenth century, would make major advances in fisheries techiques and fisheries biology. Small wonder, then, that "King Herring" held the stage, with a rather limited supporting cast of other and mainly cool-water clupeoids. In the magnificent review of clupeoid biology by Blaxter and Hunter (1982) one finds only 31 main clupeoid species listed in their table 1, and although some 70 species appear in the index, more than half of these are merely passing mentions. Quite important roles are accorded to the genera *Sprattus*, *Sardina*, *Sardinops*, *Sardinella*, *Brevoortia*, and *Engraulis*, but about 300 clupeoid species merely stand in the wings. This is not the authors' fault: they have correctly reviewed the literature and that is the result.

The clupeoid species studied are those that not only have great economic importance, but those that occur where there are the best-equipped laboratories and the best-trained workers. One can note also that the species are mostly of genera that are monotypic (or monotypic within the area fished), thus a far cry from the complex multispecies clupeoid catches of tropical regions, where 10 or more herring and anchovy species may come up in the same net. In fact, the review by Blaxter and Hunter (1982) shows that there has been a considerable neglect of the tropical clupeoids, and this is all the more unfortunate because it is largely these fishes that in the postwar years have accounted for the more than tripling of the total clupeoid catch. It is not a matter of removing the crown from *Clupea* and his cool-water colleagues — this conference well demonstrates the need for continuing biological and fisheries research on herrings — but of placing herring research in the wider context of clupeoid research, to the benefit of both.

What Is a Clupeoid?

From the literature, it might be assumed that the herring is a rather special sort of clupeoid; therefore, are the other 300 species relevant to its study? The answer is that, in their basic anatomical engineering, and thus one must presume also in certain basic aspects of their biology, the clupeoids are a remarkably close-knit group. Only quite recently, however, have sufficiently trenchant and derived (i.e. apomorph) characters been found to define the superorder Clupeomorpha, the order Clupeiformes, and its suborder Clupeoidei or clupeoid fishes.

Earlier authors, largely on the basis of primitive (plesiomorph) characters, grouped together various lower teleosts into what some (e.g. Berg, 1940, p. 417) frankly admitted to be an artificial assemblage of clupeiform fishes in which were also included elopoids (*Elops*, *Megalops*), albuloids (*Albula*), and others. The first effective challenge to this traditional classification was made by Greenwood et al. (1966), who successfully narrowed down the Clupeiformes to its present limits and further ensured its purity by creating a superorder Clupeomorpha from which even at this level the elopoid, albuloid, and other elements were expunged. Subsequent work, chiefly by palaeontologists and thus based on osteological characters, has further refined the hierarchy Clupeomorpha, Clupeiformes, Clupeoidei, best expressed by Grande (1982a, p. 19–22). The cladogram in Fig. 1 is based on Grande's conclusions, with the numbered defining characters (synapomorphies) listed in Table 1.

In Fig. 2 is shown an essential clupeoid fish. Like other *lower teleost fishes*, it has abdominal pelvic fins and lacks fin spines. In common with other *clupeomorphs*, it has a pelvic scute, if not scutes before and behind the pelvic fin and scutes along the back before the dorsal fin; also in common with other clupeomorphs, the caudal fin has the 2nd hypural plate fused with the 1st ural centrum. In common with other *clupeiforms*, it has a recessus lateralis, the parietals separated by an anterior process of the supra-occipital, the endopterygoid teeth reduced, and no "beryciform foramen" in the anterior ceratohyal. Most of these are internal characters, discoverable only by dissecting or staining. Five further characters are necessary to distinguish *clupeoids* from other clupeiform fishes. One of these is obvious at a glance, the lack of lateral line scales, but the other four define in yet more detail the osteology of the caudal fin (parhypural primitively free from the 1st pre-ural centrum, the 1st ural centrum reduced, the 1st uroneural fused to the 1st pre-ural centrum, and the 1st hypural "free" at its base).

Suites of small defining characters such as these, although in concept not new (such osteological features were especially pioneered by Regan more than 50 yr ago), have the advantage that they seem to cut across the wide range of morphological, physiological, and ethological diversity found in a group such as the clupeoids. They unite even more firmly an assemblage of fishes that seemed almost intuitively to earlier ichthyologists to form a "natural group." Moreover, these apparently minor features that are exclusive to the Clupeomorpha, the Clupeiformes, or the Clupeoidei must reflect some basic common patterns of physiology or behaviour. To discover these would be

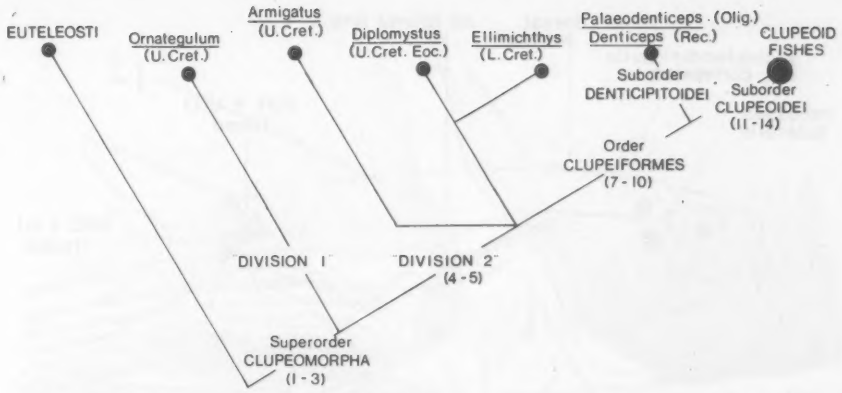

FIG. 1. Cladogram showing relationships within the superorder Clupeomorpha (adapted from Grande 1982a). Numbers refer to defining characters listed in Table 1.

to show how far our rather sophisticated knowledge of *Clupea* biology can be applied to other clupeoids.

In essence, the defining characters of clupeoid fishes discussed above centre around three main aspects of the body: (1) dorsal and ventral body profiles (i.e. scutes), (2) caudal fin skeleton, and (3) sensory canal system (head canals, but no lateral line), coupled with the swimbladder–ear connexion.

The biological implications of these have been investigated, but the full significance of caudal fin details and scute patterns remains elusive.

Scutes

The clupeomorph scute is a characteristic single-element unknown outside the group (the nearest approach is the double-element scute of the osteoglossomorph *Notopterus*). They form small and often keeled plates along the belly or back, the former usually with lateral arms (Fig. 3). All members of the Clupeomorpha, except for adult *Chirocentrus* and the Upper Cretaceous *Ornategulum* (see Forey 1973), have at least a pelvic scute between (and to some extent investing) the bases of the outer pelvic finrays. Most clupeomorphs with a pelvic scute also have a complete series of ventral scutes from the isthmus to the anus, but these are lacking in the round herrings (*Dussumieria*, *Etrumeus*, *Spratelloides*, *Jenkinsia*) and in *Engraulis* and all New World anchovies, or are lacking or represented by at most nine pre-pelvic scutes in certain pellonuline clupeids (*Congothrissa*, *Sierrathrissa*, *Gilchristella*, etc.) and in the Indo–Pacific anchovy genus *Stolephorus*; in the anchovies *Thrissina baelama* and *Papuengraulis micropinna* scutes are absent before the pectoral fin bases. Yet another variant is the W-shaped pelvic scute of round herrings (Fig. 3c). A complete series of predorsal scutes is found in the alosine clupeid *Ethmidium*, the pellonuline clupeids *Potamothrissa* and *Hyperlophus*, in the fossil clupeomorphs *Armigatus*, *Diplomystus*, and *Ellimichthys*, and in the fossil clupeids *Knightia* and *Gosiutichthys* (Grande 1982b); incomplete series occur in all Indo–Pacific engraulid genera (but in *Stolephorus* only in *S. tri* and *S. macrops*), in the dorosomatine clupeid *Clupanodon*, in the pristigasterid clupeid *Pristigaster*, and apparently in several other clupeid genera (Grande 1982a, p. 30).

If it is assumed that the clupeomorph scutes evolved once and have been variously and independently lost, then the pelvic scute must have had the most widespread functional significance (and the dorsal scutes the least). Perhaps the pelvic scute serves a different function from the rest, maybe as a structural support for the pelvic fins (Fig. 4); however, where the pelvic fins are small (*Pellona*, *Ilisha*) or absent (*Pristigaster*, *Opisthopterus*, *Neoopisthopterus*, *Odontognathus*, *Raconda*), the

TABLE 1. Defining characters within the clupeomorph fishes (see cladogram of Fig. 1), based on Grande (1982a, 1984).

Clupeomorpha

1. Base of 2nd hypural plate fused to 1st ural centrum (Fig. 6)
2. Otophysic connexion between swimbladder and ear via pre-coelomic ducts that penetrate the exoccipitals and form a pair of bony bullae in the pro-otics and usually also in the pterotics (Fig. 9)
3. Supratemporal commissural sensory canal primitively passing through the parietals and supra-occipital (Grande 1984, who pointed to its occurrence in characoids, osteoglossomorphs, and perhaps other groups and thus suspects its use as a defining character for clupeomorphs)

"Division 2" (of Grande 1982a: unnamed)

4. One or more single-element scutes along the belly, but independently lost in various groups (Fig. 3)
5. One or more single-element scutes along the back before the dorsal fin, but independently lost in various groups (Fig. 5)
6. Well-defined pre-epiotic fossa (on the floor of which can be seen the bulge of the pterotic bulla (Whitehead 1964, p. 325))

Clupeiformes

7. Presence of a recessus lateralis or chamber receiving branches of the infra-orbital, supra-orbital, pre-opercular, and temporal head sensory canals
8. Parietals completely separated in the midline by the anterior extension of the supra-occipital
9. Middle radials of anal fin apparently fused to proximal radials (Grande 1983)
10. Loss of the "beryciform foramen" in the anterior ceratohyal (Grande 1983)

Clupeoidei

11. Fusion of 1st uroneural with 1st pre-ural vertebral centrum (Fig. 6)
12. Reduction in size of 1st ural centrum
13. Base of parhypural free from 1st pre-ural centrum (Fig. 6)
14. Base of 1st hypural plate "free" (i.e. truncated and failing to articulate with a centrum, Fig. 6)
15. Loss of pored lateral line scales (shared with *Denticeps*, however)

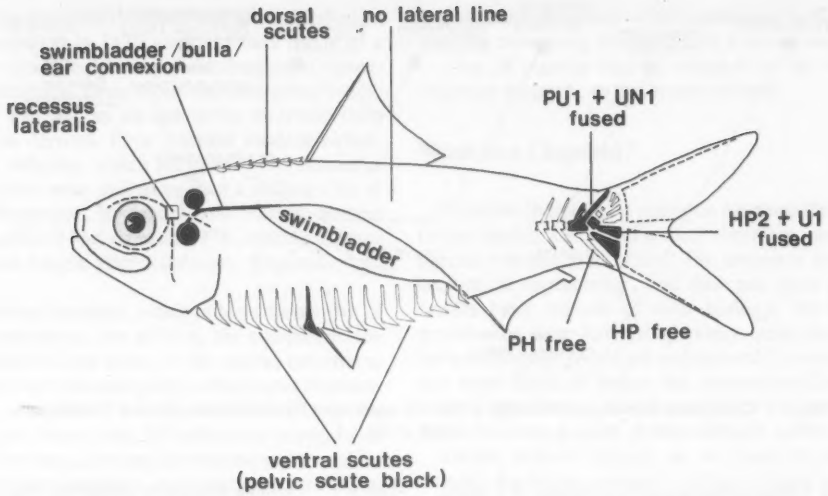

FIG. 2. Some essential features of a clupeoid fish, at least primitively. Caudal fin elements are explained in the text and in Fig. 6.

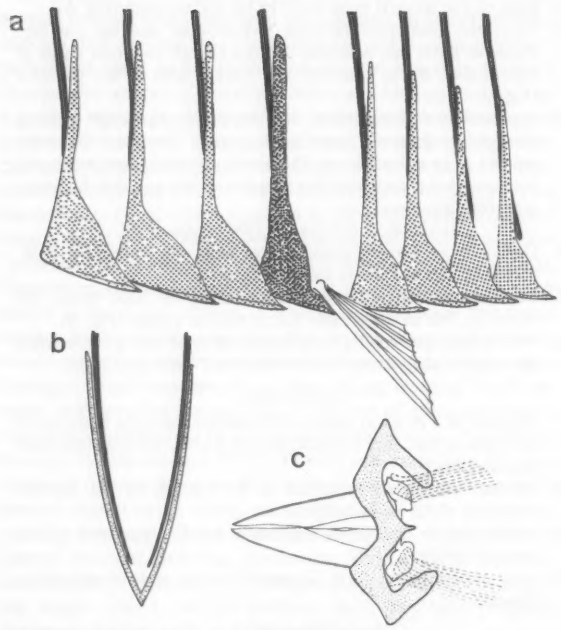

FIG. 3. (a) Typical pre- and post-pelvic clupeoid scutes (pelvic scute darker; pleural ribs black); (b) cross-section; (c) W-shaped pelvic scute in round herrings (Dussumieriinae).

pelvic scute may participate in the function of the other ventral scutes. In the more compressed clupeoids the scutes are the cutting edge of an axe-shaped body, one advantage of which is to reduce the shadow under the body to almost nothing (especially when combined with the platelets of silvery guanine under the scales that, as shown by Denton and Nicol (1965), lighten the underparts when viewed from below). Nevertheless, many quite round-bodied clupeoids (*Clupea*, *Sardina*, *Sardinella aurita*, etc.) have a full complement of rather rounded scutes, which perhaps serve another purpose (hydrodynamic, or support for pleural ribs, Fig. 3a, 3b).

Dorsal scutes can hardly serve for camouflage, fin or rib support, or hydrodynamics. They never produce a strong keel; in the engraulids they are merely a small plate with a short spine just in front of the dorsal fin, while in other clupeomorphs they are oval or rectangular plates, occasionally pectinated behind and in some species with a low median ridge (Fig. 5a, 5b). It seems likely that primitively they served the same function as the ventral scutes, but with their gradual loss the few remaining dorsal scutes may now serve a quite different purpose.

Thus, one of the most characteristic external features of clupeomorphs, the scutes, cannot yet be related to some biological feature common to the group.

Caudal Fin

In Fig. 6 is shown a typical clupeoid caudal fin skeleton. As in all clupeomorphs, the 1st hypural plate is quite free at its base, whereas the 2nd hypural base is fused to the 1st ural centrum. Characteristic of clupeoids is a further fusion of caudal elements, the 1st uroneural becoming fused to the 1st pre-ural centrum (plus its plate-like dorsal spine); at the same time the 1st ural centrum has become very reduced in size. The parhypural is free from the 1st pre-ural centrum in all except the round herring genera *Dussumieria* and *Etrumeus* (Gosline 1960: fig. 7; Grande 1983) (Fig. 7c); it is, however, firmly bedded to the centrum and must be almost rigid in the vertical field, although perhaps a little flexible horizontally.

Such small events in the caudal fin might seem merely arbitrary choices, but their constancy is impressive, as also their unique combination in clupeoids. Nevertheless, fusion of the 2nd hypural with the 1st ural centrum probably occurs also in all ostariophysans, as well as the fusion of the 1st uroneural with the pre-ural centrum. Such features must have been independently derived, and they suggest a general direction in achieving a more efficient caudal fin.

The branched caudal finrays are double elements whose bases (small knobbed plates in clupeoids) clamp on either side of the hind edges of the hypural plates to make a firm but flexible

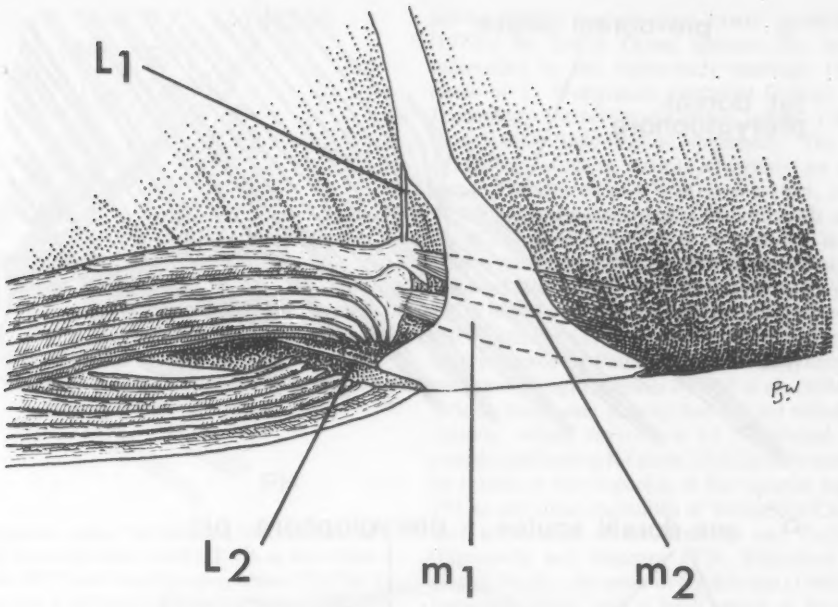

FIG. 4. Clupeoid pelvic scute showing bracing with ligaments (L_1 and L_2) and passage of the adductor muscles for the 1st finray beneath the scute arms (m_1 and m_2).

hinge. In fact there is a double-hinge, since the bases of the hypural plates are usually free within the fairly rigid V formed by the uroneurals above and the parhypural below, the two arms meeting at the 1st pre-ural centrum. Since of all fins the tail beats virtually continuously throughout life in pelagic fishes such as clupeoids, even the most minute details of the skeletal framework must be functionally significant. The clupeoid solution is not, of course, the only one, being merely a modification on the inherited clupeomorph pattern, but its efficiency is undoubted. Nevertheless, refinements are possible. In five species of the Indo–Pacific anchovy genus *Stolephorus* the 2nd hypural is not only fused to the 1st ural centrum (as in all clupeoids), but the latter is also fused to the 1st pre-ural centrum (i.e. the crux of the V) (Fig. 7b). The 1st hypural is thus sandwiched between two fairly inflexible rods (2nd hypural above and parhypural below), which presumably allows the lower half of the caudal fin to beat more strongly than the upper. Other and functionally unrelated characters separate these five species of *Stolephorus* (*S. punctifer*, *S. heterolobus*, etc.) from their congeners (G. J. Nelson and P. J. P. Whitehead, in prep.). Are their swimming habits and other aspects of their biology different also? This additional fusion also occurs in *Engraulis*, all New World anchovies, and in two dussumieriines (*Spratelloides* of the Indo–Pacific, *Jenkinsia* of the western Atlantic) as well as in most freshwater African pellonulines and in the European clupeine *Clupeonella cultriventris* (Grande 1983). Presumably this fusion was independently derived, but is there a common functional basis?

The use of very small details of caudal osteology in defining relationships has not yet been followed up by equally detailed functional comparisons. The most that can be said is that the clupeoid caudal fin is distinctive and that what is known of its functioning in *Clupea* can probably be extrapolated to other species.

Swimbladder–Bulla–Head Canal System

In all clupeiform fishes (and presumably in all clupeomorphs, as far as can be judged from the fossils) the physostomous swimbladder has a pair of anterior tubular extensions that penetrate the skull (through the exoccipitals) and expand into partially gas-filled capsules invested by bony bullae within the pro-otics; in almost all clupeoids a second pair of similar bullae occur in the pterotics (absent only in the clupeid clupeines *Sprattus* and *Clupeonella*, and in the clupeomorph *Spratticeps* of the Upper Cretaceous according to Patterson 1970; rather small in some clupeids and engraulids, however). The lower two thirds of the pro-otic bullae are filled with gas (from the swimbladder through the pre-coelomic ducts and via the pterotic bullae if present), wheras the upper third is separated off by a membrane and is filled with perilymph via a small fenestra opening into the perilymph space surrounding the labyrinth of the ear. The fenestra is just below the utricular maculae and, at least in *Clupea harengus* and *Sprattus sprattus*, an elastic thread passes through the fenestra to join the maculae to the pro-otic membrane (Best and Gray 1980; Blaxter et al. 1981). The system is shown diagrammatically in Fig. 8.

An integral part of this otophysic system, as first fully described by Wohlfarht (1937) and explained by Denton and Blaxter (1976), is the recessus lateralis characteristic only of clupeiformes. The recessus is a small chamber into which open four sensory canals of the head: the infra-orbital, supra-orbital, pre-opercular, and temporal canals. These canals are in places covered by bone (e.g. under and behind the eye) but for the most part are cutaneous canals that ramify and anastomose over the head, the floor of the main parts bearing neuromasts at intervals. Characteristic also of clupeiformes is the absence of lateral line scales down the flanks (although one or two may occur just behind the gill opening in a few species).

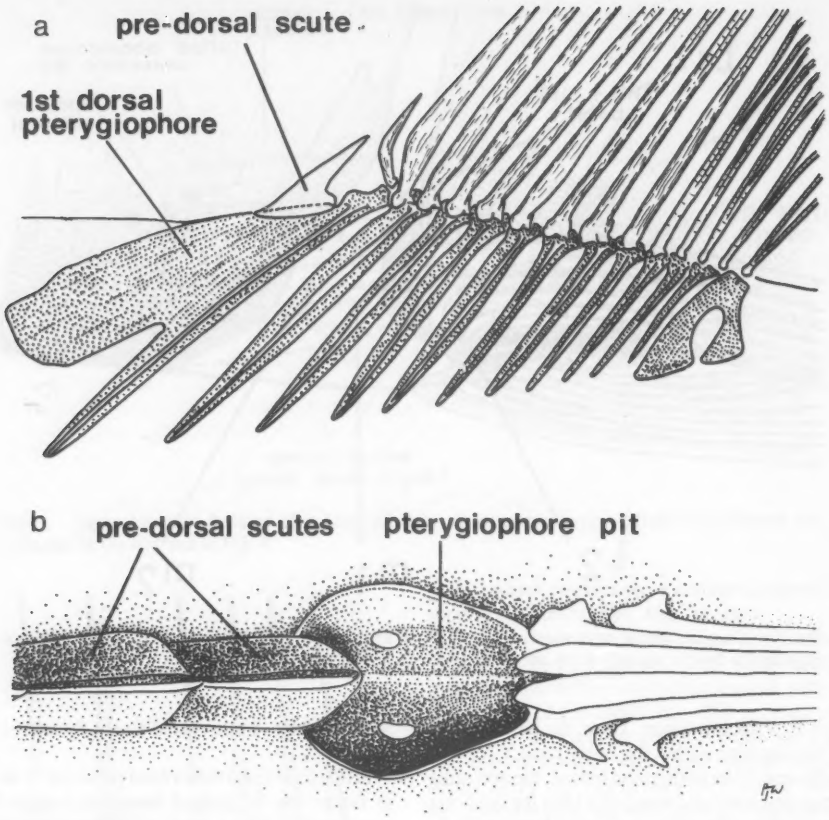

FIG. 5. (a) Lateral view of pre-dorsal scute in most Indo–Pacific anchovies (*Setipinna taty*); (b) dorsal view of the final two pre-dorsal scutes in *Potamalosa richmondia*. In Indo–Pacific anchovies the single pre-dorsal scute straddles the small surface pit of the 1st dorsal pterygiophore.

The importance of the head canal system lies in the close approximation of the recessus to the otic region, the inner wall of the recessus being a compliant membrane abutting the perilymph space. In effect, this means that any variations in pressure within the recessus will be transmitted via the perilymph to the utricular maculae, quite apart from stimulating the neuromasts within the canals themselves. The entire system is shown diagrammatically in Fig. 9.

The best description of this extremely complex system is that given by Blaxter and Hunter (1982, p. 147–152). They supposed that the swimbladder serves a minor role in buoyancy, acting rather as a reservoir or sink that cushions large gas pressure differences in the pro-otic bullae (which could burst the membrane or flex it beyond optimum sensitivity), yet allows differences to be felt and thus transmitted to the utricular maculae. Movement of the pro-otic bulla membrane would also flex the membrane of the recessus, thus presumably stimulating the neuromasts via movements of liquid in the head canals. At the same time, the neuromasts themselves would also be directly affected by particle diplacements in the liquid of the canals via the exterior pores. Blaxter and Hunter concluded that clupeoids can appreciate differences (but not absolute values) of pressure, and that by resolving the various separate signals from this intricate swimbladder–bulla–head canal coupling, they can also appreciate sound source range measurements.

A recessus lateralis occurs in the fossil clupeid genera *Knightia* and *Gosiutichthys* (Grande 1982b), which also lack lateral lines scales; thus, one must assume that this ingenious sensory system has operated since at least early Eocene times and must reflect a very basic pattern in clupeoid biology. The most obvious pattern is schooling, the *point d'appui* as it happens for fisheries. The extraordinary "discipline" of schooling clupeoids cannot be entirely due to visual stimuli.

Clupeoid Taxonomy

The suborder Clupeoidei contains at least 330 species, of which some have still to be described and named; more may as yet be found, either in such relatively unexplored areas as the tropical South American freshwaters or through more careful assessment of apparently widespread species in the seas. Linnaeus and his contemporaries had no conception of the range and diversity of the clupeoids (Table 2). In the *Systema naturae*, seven clupeoid species are placed in the genus *Clupea* (plus two non-clupeoids and one doubtful) and another in the genus *Esox* (*Anchoa hepsetus*) (Linnaeus 1758, p. 314, 317–320). A century later, *Clupea* still served as a catchall, at least for Günther (1868), who assigned no less than 60 clupeoids to this genus. Across the Channel, however, Cuvier (1816, 1829) and more especially Valenciennes (1847, 1848) had begun the

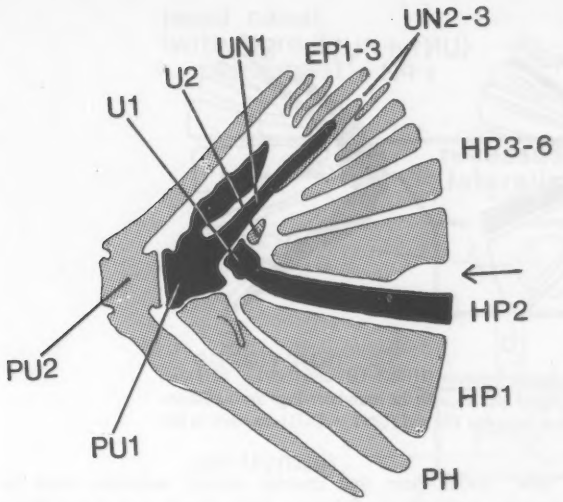

FIG. 6. Typical clupeoid caudal fin skeleton. Note fusion of 1st uroneural (UN1) with the 1st pre-ural vertebra (PU1), as also fusion of the 2nd hypural plate (HP2) with the 1st ural vertebra (U1).The 1st hypural plate (HP1) is free at its base, as also the parhypural (PH). The epurals (EP) are primitively three, the uroneurals (UN) three, and the hypurals (HP) six. Arrow shows separation of upper from lower caudal finrays, with a small gap formed by cutout in 3rd hypural.

steady splitting of the known clupeoid species (138 by 1848) into numerous genera and the assembling of these genera into what amounted to subfamilies (Whitehead 1967, p. 7–10). After another century and with the number of known species more than doubled, it was generally accepted that the clupeids and engraulids belonged to separate families, as also the round herrings (Dussumieriidae) and the wolf herrings (Chirocentridae). Based upon the clupeid papers of Regan (1916, 1917a, 1917b, 1917c, 1922) and Norman (1923), the Clupeidae was split into five subfamilies: Clupeinae, Pellonulinae, Alosinae, Dorosomatinae, and Pristigasterinae. Subsequently (Whitehead 1973a, p. 12), two further subfamilies were proposed, the Dussumieriinae and the Spratelloidinae, taken from the family Dussumieriidae of Whitehead (1963). At the same time, the Engraulidae was split into the subfamilies Engraulinae and Coilinae (Whitehead 1973b, p. 166). Serious doubts about this arrangement, its hierarchical structure, and the individual boundaries of the subfamilies have been expressed, especially by Nelson (1967, 1970) on the basis of the hyobranchial apparatus and by Grande (1983) on a whole suite of hitherto little-explored characters. Both authors favoured raising the chirocentrids, clupeids, and engraulids to superfamily status, with a fourth superfamily for the pristigasterines; in addition, Grande reunited the spratelloidines with the dussumieriines. This scheme is shown in Table 3, with an indication of the principal genera included in each group. Much more work is required, however, before the limits and definitions of the subfamilies can be stated with certainty.

Rather more immediate and practical problems, however, concern the diagnoses of species, since no biological or fisheries research is fully trustworthy unless the species studied have been both identified properly and named properly. No overall taxonomic guide exists for this purpose and even at regional level there are gaps. The review of Indo–Pacific clupeoids by Fowler (1941) was to some extent updated by Whitehead (1973b) for Indian Ocean species; this in turn has been superceded by the enormously thorough 1980 two-volume thesis of T. Wongratana (Imperial College of Science and Technology, University of London, unpubl.), based on study of some 14 000 Indo–Pacific specimens. The western Indian Ocean and southern African clupeoids are now fairly well known (Whitehead and Wongratana 1984, in press) and the surprisingly numerous Australian clupeoids are under review (T. Wongratana and P. J. P. Whitehead, in prep.). For the eastern Atlantic and Mediterranean region the species are also quite well diagnosed, those of West Africa by Whitehead (1981, and in prep.) and for the area to the north by Svetovidov (1952) and Whitehead (1984). The West African freshwater clupeids were reviewed by Poll (1974), and full synonymies and literature were brought together by Poll et al. (1984).

Such taxonomic activity has not yet tidied up the western Atlantic, where the review by Hildebrand (1963, but had awaited publication for about 15 yr) is only partially superceded by studies of the clupeoids of the Guianas region (Whitehead 1973a) and some engraulids of Venezuela (Cervigón 1969), as well as reviews of the Brazilian and Caribbean clupeoids (Figueiredo and Menezes 1978; Whitehead 1978). For the eastern Pacific, the work of Hildebrand (1946) was updated by Peterson (1956), and a fresh attack is being made on the anchovies by Nelson (1983 and in progress).

The situation is considerably better than it was 20 or even 10 yr ago, but there remain quite serious problems, often with genera or species of prime economic importance. Thus, the widespread *Sardinella aurita* is distinguished in the western Atlantic from an almost identical but high-gillraker form, which is designated *S. brasiliensis*; the former has straight, the latter strongly curled, epibranchial gillrakers on the 3rd and 4th arches (Whitehead 1978). Straight and curled gillraker forms also occur in the Mediterranean and off West Africa, where only *S. aurita* is recognised. Are two species really present in all these areas, or merely two ecophenotypes, and to what extent does this affect interpretation of all previous biological and fishery records? Can the problem be solved by electrophoretic analysis? New Zealand sprats, long regarded as a single species (*Sprattus antipodum*) that varied in body form, were recently separated into two groups on protein differences (especially lactate dehydrogenase) that correlated with body depth (Smith and Robertson 1981); armed with this clue, small but trenchant morphological differences were then found that confirmed that *S. muelleri* is the second (and more common) sprat species in New Zealand waters (Whitehead et al., in press). Similar problems, especially in the Indo–Pacific with species of *Sardinella* and *Thryssa*, or in the tropical western Atlantic with species of *Anchoa* and *Anchoviella*, might be solved in this way, but rather infrequently are there local laboratories equipped to undertake careful gel electrophoresis.

While sound taxonomy is a sine qua non for all biological and fishery studies, the taxonomy falters without a sound nomenclature, which means typification of the taxa and strict adherence to the rules of zoological nomenclature by way of investigating authorship, dating, and validity of all nominal taxa. Fortunately, most of this has now been done for clupeoids through studies of major authors such as Lacepède, Cuvier, and Valenciennes (Whitehead 1967), Bleeker (Whitehead et al. 1966), Bloch and Schneider (Whitehead 1969), Steindachner (Whitehead 1970), Day (Talwar and Whitehead 1971), etc. Nevertheless, some assumptions about the status and true

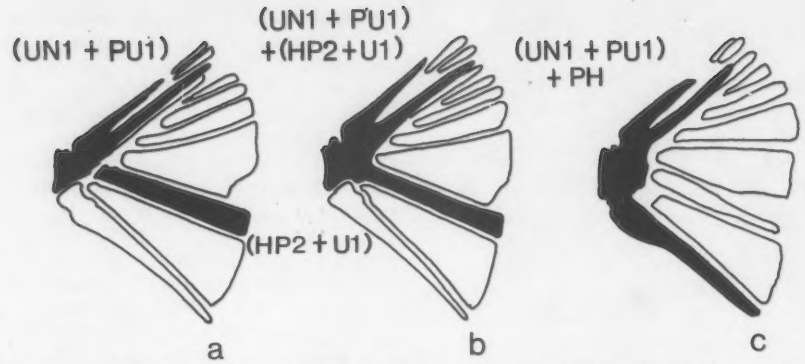

FIG. 7. (a) Typical clupeoid caudal fin skeleton; (b) fusion between (HP2 + U1) and (UN1 + PU1), as seen in the anchovies *Stolephorus punctifer* and four related species; also the round herrings *Spratelloides* and *Jenkinsia* and the clupeine *Clupeonella*; (c) fusion between PH and (UN1 + PU1), as seen in the round herrings *Dussumieria* and *Etrumeus*.

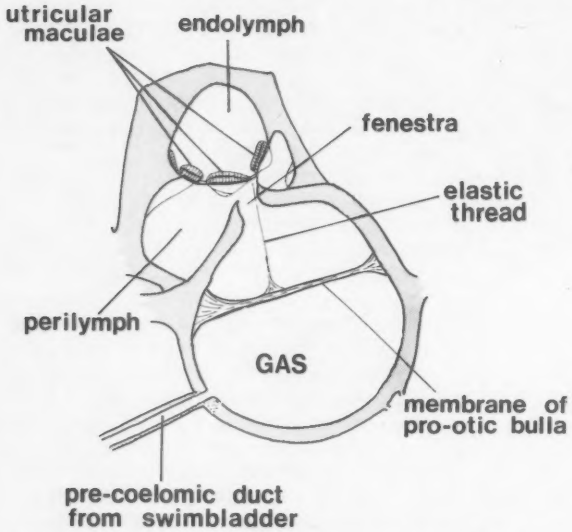

FIG. 8. Diagrammatic cross-section through pro-otic bulla and utriculus in a clupeoid fish (*Spratus*) showing separation of gas from perilymph by the pro-otic membrane and connexion of the membrane to the utricular maculae by a thread (adapted from Blaxter and Hunter 1982: fig. 48).

identity of some actual or supposed types must still be verified before the nomenclature of clupeids can be deemed sound.

A final and much neglected area concerns fossil clupeoids, where decades of assigning species to genera that are no better diagnosed than in Günther's day have wrought havoc and probably obscured a great deal of useful phylogenetic information from the 80 or so species known.

In summary, the taxonomy of clupeoid fishes, although as advanced as in many other fish groups with more than 300 species, is still not sufficient considering the economic importance of the group and thus the need for even more extensive biological studies.

Clupeoid Diversity

Quite apart from the small and mainly internal characters that distinguish the clupeoids as a group, these fishes usually have a "look" about them that enables fishery workers, even in complex multispecies fisheries, immediately to separate them out as at least "herrings" or "anchovies." Nevertheless, the clupeoids show a surprising diversity within what would seem to be a rather stylized *bauplan*.

A very obvious diversity occurs in body shape (Fig. 10, 11). *Clupea harengus* is fusiform and in cross-section oval, a form often found among clupeines, pellonulines, alosines, and engraulines, but always with a tendency for some species or genera to deepen the body and, where scutes are present, to sharpen the keel along the belly. Species of *Sardinella* show a complete series, from the almost round-bodied *S. aurita* to the deep and compressed *S. brachysoma*, and this trend is repeated to some extent in the Indo–Pacific *Herklotsichthys* (*H. quadrimaculatus* to *H. koningsbergeri*) and the engrauline genus *Stolephorus* (*S. indicus* to *S. tri*). An almost cyclindrical body is found in the round herrings (especially *Dussumieria* and *Etrumeus*) and it is noticeable that certain other clupeoids that either lack scutes or have them feebly developed also tend to have round bodies (pellonulines such as *Congothrissa*, *Sierrathrissa*; anchovies such as *Engraulis* and some *Stolephorus* and *Anchoa*). If compression and deepening of the body are a trend, then it occurs within the dorosomatines (*Clupanodon* to *Nematalosa* to *Anodontostoma*, the latter sometimes as deep as long), the engraulines (*Stolephorus* and *Thrissina* through *Thryssa* to *Setipinna* and *Papuengraulis*), and especially among the pristigasterids, the "end result" being *Pristigaster* (Fig. 10e) with a shape not unlike *Gasteropelecus*. No intermediates occur, however, for the most striking departure from the presumed normal shape, the extraordinary tapering of the body in the rat-tailed engraulid genus *Coilia* (Fig. 11f), which closely approximates to a macrourid.

The disposition, shape, and size of the fins is fairly closely correlated with body shape, at least within what appear to be the limits of particular genera, tribes, or subfamilies. The dorsal fin is always short and usually near the midpoint of the body, but it tends to move backward in the compressed but elongate forms, e.g. *Chirocentrus*, *Odontognathus*, and *Opisthopterus*, as also in the anchovies *Lycengraulis* and especially *Pterengraulis*; at the same time, the dorsal fin becomes smaller and in the Indo–Pacific *Raconda* is totally absent. The pelvic fins are small and are inserted just before, below, or just behind the dorsal fin base, with a tendency to lie farther forward as the length of the anal fin increases; the number of finrays (which

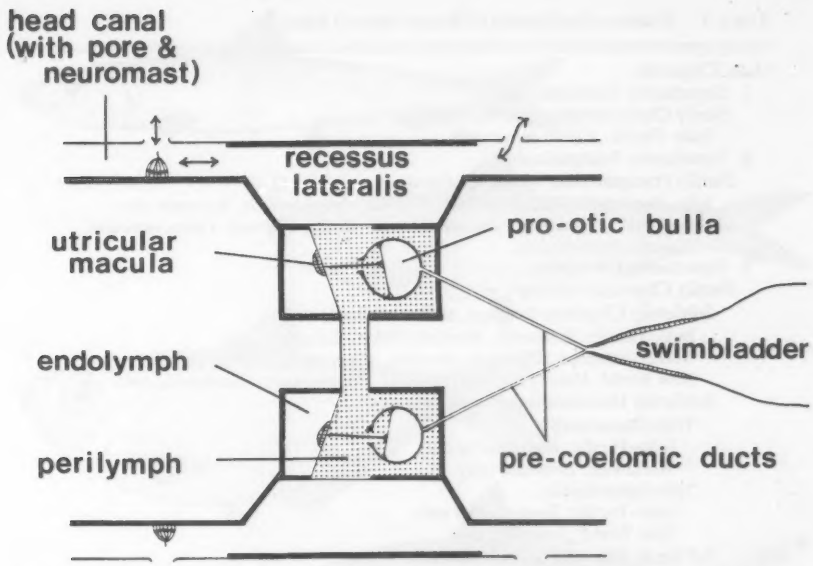

FIG. 9. Typical clupeoid otophysic connexions between the swimbladder, pro-otic bullae, ear, recessus lateralis, and head canal system (adapted from Denton and Blaxter 1976: fig. 1).

TABLE 2. Approximate numbers of Recent clupeoid fishes for major geographical areas (percentage endemism shown in parentheses).[a]

	Indo–Pacific	Eastern Atlantic	West Africa (freshwater)	Western Atlantic	Eastern Pacific
Chirocentridae					
Total					
Genera	1				
Species	2				
Endemic					
Genera	1(100)				
Species	2(100)				
Clupeidae					
Total					
Genera	31	9	13	20	12
Species	104	21	22	40	19
Endemic					
Genera	24(77.4)	4(44.4)	13(100)	11(55.0)	2(16.7)
Species	100(96.1)	17(80.9)	22(100)	37(92.5)	16(84.2)
Engraulidae					
Total					
Genera	8	1		8	6
Species	62	1		37	30
Endemic					
Genera	7(87.5)	0		3(37.5)	0
Species	62(100)	0		34(91.9)	29(96.6)
All clupeoids					
Total					
Genera	40	10	13	28	18
Species	168	22	22	77	49
Endemic					
Genera	32(80.0)	4(40.0)	13(100)	14(50.0)	2(11.1)
Species	164(97.6)	17(72.2)	22(100)	71(92.2)	45(91.8)

[a]Totals for families: Chirocentridae: 1 genus, 2 species; Clupeidae: 55 genera, 179 species; Pristigasteridae: 9 genera, 17 species; Engraulidae: 15 genera, 128 species; all clupeoids: 80 genera, 326 species.

TABLE 3. Tentative classification of Recent clupeoid fishes.

Order Clupeoidei
1. Superfamily Chirocentroidea
Family Chirocentridae (wolf-herrings)
Indo–Pacific: *Chirocentrus* only
2. Superfamily Pristigasteroidea
Family Pristigasteridae (pristigasterines)
Indo–Pacific: *Ilisha* (also Africa), *Pellona*, *Opisthopterus*, *Raconda*, etc.
New World: *Pristigaster*, *Odontognathus*, (*Ilisha*, *Pellona*), *Chirocentrodon*, *Neoopisthopterus*, etc.
3. Superfamily Clupeoidea
Family Clupeidae (herrings)
Subfamily Clupeinae (herrings, sprats, sardines, etc.)
Indo–Pacific: *Sardinella*, *Herklotsichthys*, *Escualosa*, etc.
Boreal, antitropical: *Clupea*, *Sprattus*, *Clupeonella*, *Sardinops*, etc.
New World: *Harengula*, *Opisthonema*, *Ramnogaster*, (*Sardinella*), etc.
Subfamily Dussumieriinae (round herrings)
Tribe Dussumieriini
Indo–Pacific: *Dussumieria* only
Worldwide: *Etrumeus* only
Tribe Spratelloidini
Indo–Pacific: *Spratelloides* only
New World: *Jenkinsia* only
Subfamily Pellonulinae (pellonulines)
Tribe Pellonulini
Indo–Pacific: *Gilchristella*, *Dayella*, *Ehirava*, etc.
W. Africa: *Pellonula*, *Stolothrissa*, *Sierrathrissa*, *Microthrissa*, *Congothrissa*, etc.
New World: absent
Tribe Hyperlophini (double-armoured herrings)
Australia: *Hyperlophus*, *Potamalosa* only
Subfamily Alosinae (shads)
Indo–Pacific: *Hilsa*, *Tenualosa*, *Gudusia* only
Europe: *Alosa* only
W. Africa: *Ethmalosa* only
New World: *Pomolobus*, *Brevoortia*, (*Alosa*); also *Ethmidium* (E. Pacific)
Subfamily Dorosomatinae (gizzard shads)
Indo–Pacific: *Nematalosa*, *Gonialosa*, *Anadontostoma*, *Clupanodon*, etc.
New World: *Dorosoma* only
4. Superfamily Engrauloidea
Family Engraulidae (anchovies)
Subfamily Engraulinae
Indo–Pacific: *Stolephorus*, *Thryssa*, *Setipinna*, (*Engraulis*), *Lycothrissa*, etc.
Europe, W. Africa: *Engraulis* only
New World: (*Engraulis*), *Anchoviella*, *Anchoa*, *Cetengraulis*, *Lycengraulis*, etc.
Subfamily Coilini (rat-tailed anchovies)
Indo–Pacific: *Coilia* only

determines the spread of the pelvic fins) varies from i 5 to i 10, but is surprisingly constant within many genera, some subfamilies, and throughout the Engraulidae (i 6, except for *Coilia ramcarati* with i 8–9); the disappearance of the pelvic fins in *Pristigaster* and four other pristigasterid genera was noted already. The pectoral fins vary little, but tend to have a stronger upper finray and to be more expanded in the highly compressed but elongate clupeoids (*Chirocentrus*, *Opisthopterus*, *Pterengraulis*, etc.). The anal fin is highly variable, tending to be shortest in round-bodied species (*Etrumeus* i 7–8, *Dussumieria* i 10–13) and longer or very long in the strongly compressed species (more than 30 branched finrays in pristigasterids, iii 28–31 in *Pterengraulis*, and 50 or more branched finrays in *Setipinna*; *Coilia* has 80 or more). The caudal fin is forked, except in *Coilia* (pointed), and varies only a little in the size of the lobes and the rounding or pointing of their tips. The last dorsal finray is a long filament in most gizzard shads and in the clupeine *Opisthonema*; such a filament also occurs in the quite unrelated tarpons *Tarpon* and *Megalops*. The 1st pectoral finray is produced as a filament in the western Atlantic *Anchoa filifera* (but not in the almost identical *A. lyolepis*) and in the Indo–Pacific *Setipinna*; in *Coilia* the upper 6–19 pectoral finrays are long filaments. In *Tarpon* the dorsal filament sweeps across the back from side to side as the fish swims, perhaps smoothing out turbulence, but I have not observed the action of the clupeoid pectoral filaments.

Diversity in body form and fins, presumably mainly adaptations to various kinds of swimming, are paralleled by diversity in mouth shapes, teeth, and guts, reflecting a very wide range of diet. *Clupea* has what might be termed a typical clupeid mouth, with triangular pre-maxillae, maxillae that expand distally and along their upper edge bear two supra-maxillae, and an almost triangular lower jaw with a deep coronoid process (Fig. 12a). The mouth is terminal or the lower jaw slightly projecting.

FIG. 10. Variations in general clupeid form, from slender and almost cylindrical to highly compressed and deep or elongate. a, *Etrumeus teres*; b, *Sardinella aurita*; c, *Pellona harroweri*; d, *Opisthonema oglinum*; e, *Pristigaster cayana*; f, *Odontognathus compressus*.

Gross variations on this are the protrusion of the lower jaw tip in pristigasterids (*Pellona*, *Ilisha*) until the mouth is pointing upward (*Opisthopterus*, *Odontognathus*, Fig. 12b) and the shortening and widening of the lower jaw in dorosomatines (*Clupanodon*, *Konosirus*) until the mouth is fully inferior (*Nematalosa*, *Dorosoma*). Minor variations are the loss of the anterior supra-maxilla (consistently so in all pellonulines) the shortening and narrowing of the maxilla in dorosomatines, the extension of the maxilla in *Odontognathus* to reach the gill opening (Fig. 12b), and the addition of a small and toothed hypo-maxilla in *Pellona* and *Harengula* between the pre-maxilla tip and the lower bulge of the maxilla. The engraulid mouth is "underslung," the articulation of the lower jaw far back behind the eye, and both maxilla and dentary are long and slender (Fig. 12d). In the Indo–Pacific *Setipinna* the lower jaw tends to protrude until the mouth is pointing upward in *S. breviceps*, while in the western Atlantic *Anchoviella* the maxilla shortens until an almost clupeid mouth is produced in *A. brevirostris* (Fig. 12f). Anchovies also tend to lose the anterior supra-maxilla, and a parallel trend toward extension of the maxilla tip occurs in both New World and Indo–Pacific genera (*Anchoa* and *Thryssa*), with the maxilla tip surpassing the anal fin origin in *T. setirostris* (which alone of all engraulines has a high coronoid process; almost as high in *Coilia* also).

Small or minute conical teeth are typically present in both herrings and anchovies in a single series along the jaws and scattered on the vomer, palatines, and endo- and ecto-pterygoids, but there is great variation. At one extreme are the

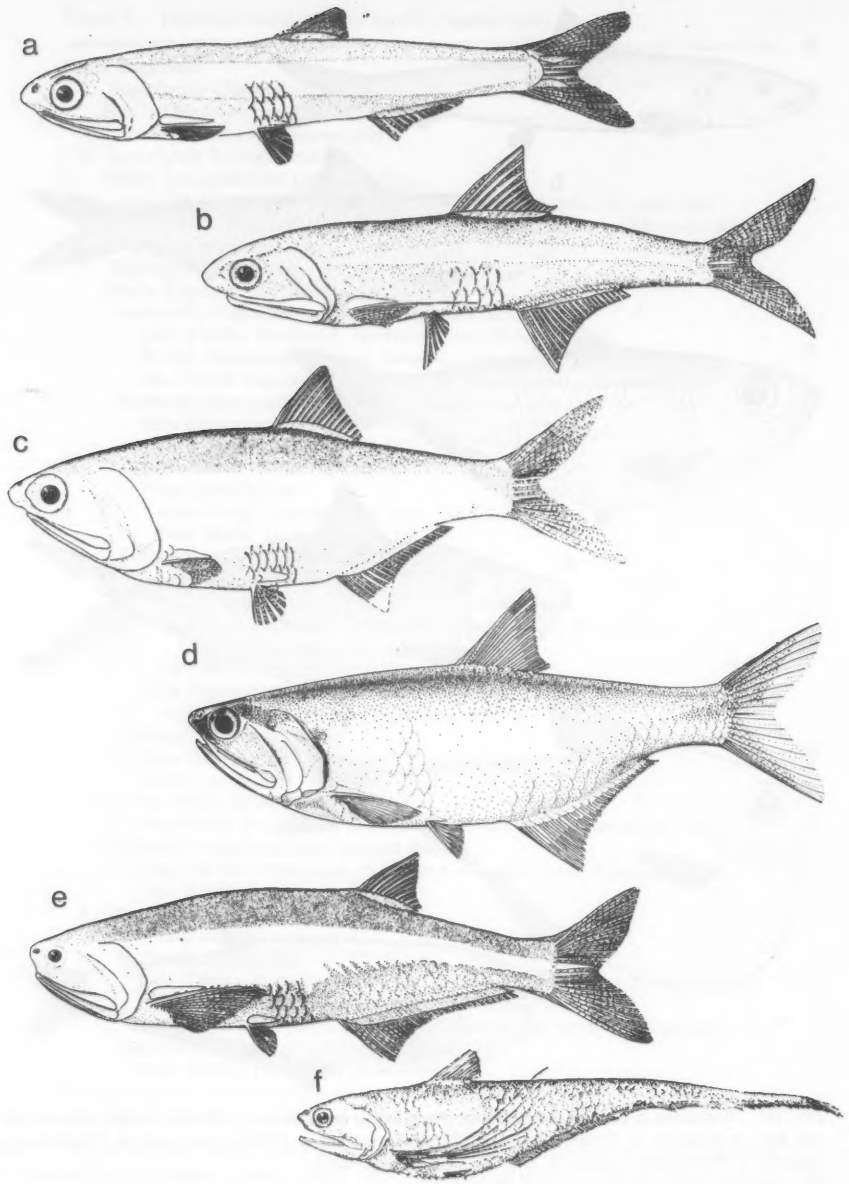

FIG. 11. Variations in general engrauloid form, from slender and almost cylindrical to highly compressed and rat-tailed. a, *Engraulis eurystole*; b, *Anchoa filifera*; c, *Cetengraulis edentulus*; d, *Anchovia surinamensis*; e, *Pterengraulis atherinoides*; f, *Coilia neglecta*.

canine teeth of *Chirocentrus* and also the New World *Chirocentrodon* (Fig. 12c, 13), repeated (as far as the engraulid mouth will allow) in the Indo–Pacific *Lycothrissa* and the New World *Lycengraulis* (Fig. 12e). At the other extreme are the toothless dorosomatines and the New World engraulid *Cetengraulis*. Small tooth-plates are also found on the gill arches and apparently quite independently have developed also on the upper edge of the ceratohyal in the New World *Pterengraulis*, some species of *Anchoa*, and the Indo–Pacific *Stolephorus tysoni*; soft, fleshy "teeth" occur here also in *Sardina* and *Sardinops*.

As in other fishes, the gut ranges from short and straight in piscivores (*Chirocentrus*, etc.) to long, looped, and coiled in microphagus feeders (dorosomatines, etc.). Similarly, gill-rakers may be as few as 20 (some *Lycengraulis*) or as many as several hundred (*Sardinella aurita*) or more (gizzard shads), usually with a concomitant increase in numbers of pyloric caeca (less than 10 to over 200). Some clupeids, especially the

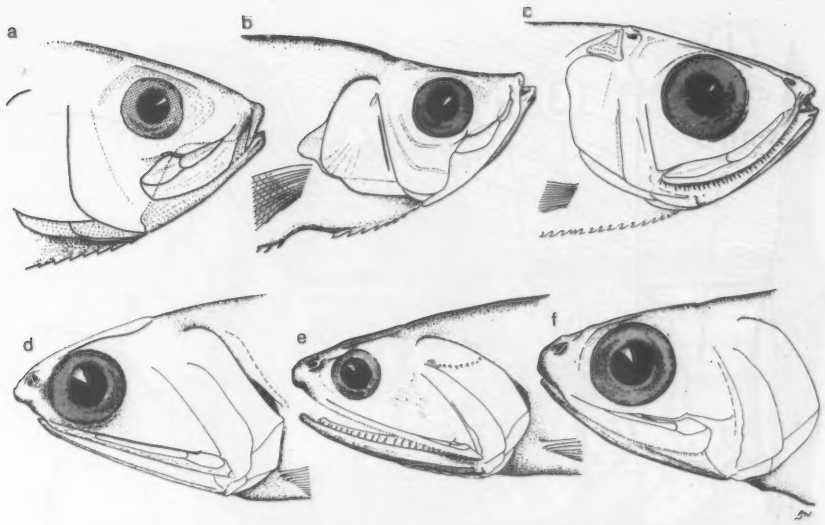

FIG. 12. Mouth shapes in clupeids (upper) and engraulids (lower). a, Typical clupeine; b, *Odontognathus mucronatus*; c, *Chirocentrodon bleekerianus*; d, typical engrauline; e, *Lycengraulis batesii*; f, *Anchoviella brevirostris*.

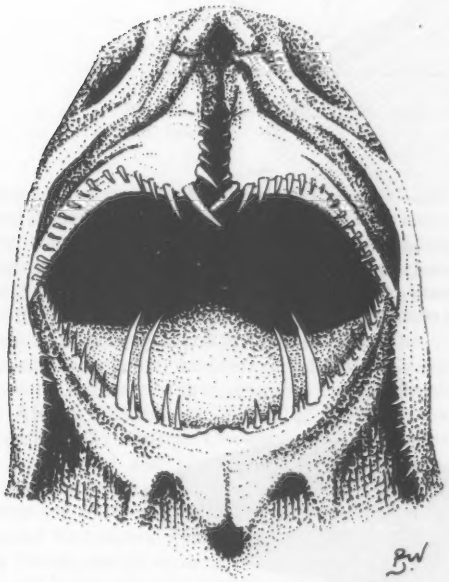

FIG. 13. Mouth of *Chirocentrodon bleekerianus* from front showing canine teeth and separation of pre-maxillae, which bear small teeth in the midline.

dorosomatines, have pharyngeal pouches (epibranchial organs) associated with the 4th epibranchial, which are believed to concentrate food from the very numerous gillrakers and evert it as a bolus down the pharynx.

Whether or not *Clupea harengus* should be considered the "norm" for clupeids (and *Engraulis encrasicholus* perhaps for engraulines), the extensive and often highly detailed studies of *Clupea* (and to a lesser degree *Engraulis*) will for long serve as a comparative basis when exploring all the many other variations on the clupeoid theme. Why, for example, do some small clupeids and engraulids have a silver stripe down the flank? In *Stolephorus heterolobus* among others it covers (but not very exactly) the red muscle, which itself has a layer of guanine below (Fig. 14). Unique among clupeoids are the light organs of *Coilia dussumieri*, which form a series down the flanks and even extend onto the isthmus (Fig. 15, 16); in spite of their deceptively deepwater appearance, these fishes live in shallow water, usually in rather turbid estuaries. Less spectacular but no less interesting are variations in swimbladder shape (e.g. with one or a pair of postcoelomic tubes in species of the pristigasterid genus *Ilisha*), as well as its exit (or not) at the anus, and the point at which the pneumatic duct joins the gut (before or from the stomach blind sac). The notched upper jaw in shads and some gizzard shads, contrasted with the rounded upper jaw when seen from the front in most clupeids, has never been explored in functional terms, nor indeed has the arrangement of ligaments and articular facets been described properly for other clupeid mouth shapes. The description of these and the many other so-called "departures" from the clupeoid norm, both in morphological and functional terms, will not only rest on *Clupea* and *Engraulis* studies, but may well hint at functions and origins hitherto unsuspected in the better known species.

The clupeoids are typically small or moderate-sized coastal marine fishes. A minority of genera contain some or all species that reach or exceed 30 cm SL (*Clupea*, *Alosa*, *Pomolobus*, *Tenualosa*, *Pellona*, *Chirocentrus*, etc.); among the largest species are *Chirocentrus dorab* (to 100 cm), *Tenualosa ilisha* (to 60 cm), *Pellona flavipinnis* (to about 45 cm), and for anchovies *Thryssa scratchleyi* (to 30 cm). For the majority of clupeoid genera the adult size is about 10–20 cm SL (some Dussumieriinae, some Pellonulinae, Clupeinae such as *Harengula*, *Herklotsichthys*, most *Sardinella*, *Sprattus*, *Sardinops*, *Sardina*, and so on, and most anchovies). Among the small clupeoids are members of *Spratelloides*, *Jenkinsia*, *Ramnogaster*, most Pellonulini, and for anchovies most members of *Anchoa*, *Anchoviella*, and *Stolephorus*, with an adult size of

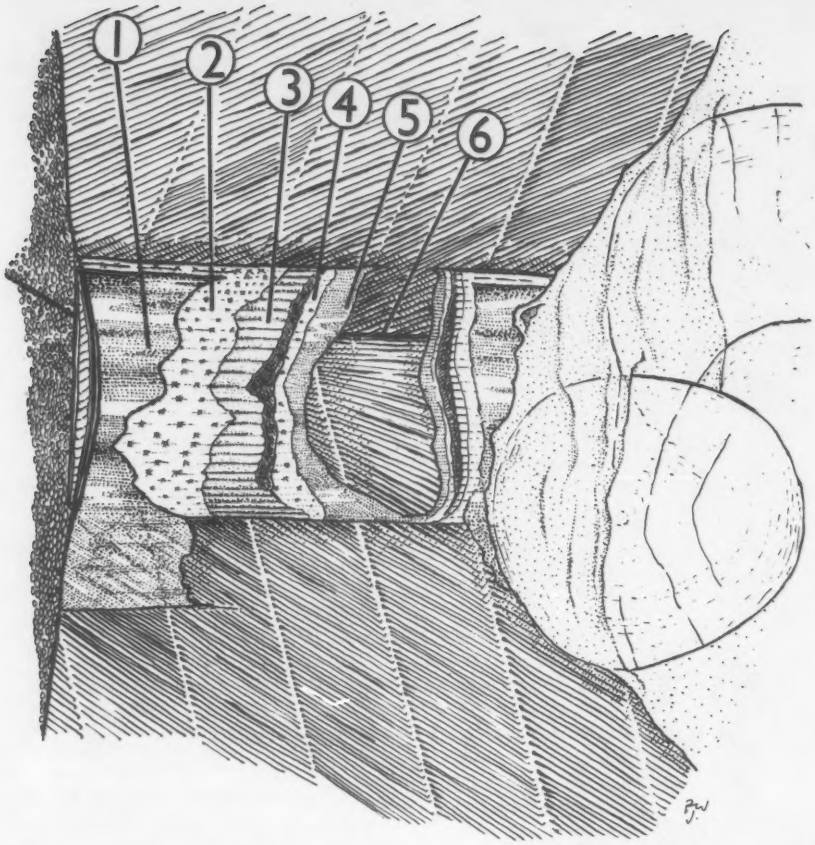

FIG. 14. Left flank of *Stolephorus heterolobus* dissected to show the silvery midlateral stripe (1), which overlies the longitudinal band of red muscle (3), the latter invested in a pigmented sheath (2 and 4) and underlain by a second silvery (guanine) layer (5). Neither the silvery stripe nor the band of red muscle are exactly centred over the horizontal myoseptum (6). Scales and remnants of epidermis on right.

FIG. 15. *Coilia dussumieri* (155 mm SL) showing light organs on flanks. The fish on capture is light brownish (blue–grey on back) and the light organs are golden fading to silver.

5–10 cm. Pygmy species are rare and are only found in freshwaters of southeast Asia (some *Clupeoides*, *Clupeichthys* spp.), West Africa (*Thrattidion noctivagus* to 2.1 cm, *Sierrathrissa leonensis* to 2.5 cm), and in the Amazon (new species to be described by Roberts (in press), mature at only 1.5 cm, one of several endemic pygmy anchovies of South American rivers).

Although the clupeoids are typically a marine group (and presumably had a marine origin), they seem to have been rather frequently tempted into estuaries and rivers. Perhaps significantly, it is the larvae and young stages that seem most resistant to low salinities (Holliday 1969), but adults of a number of marine clupeoids are surprisingly euryhaline. Races of *Clupea harengus*, for example, occur in the open ocean and also in the upper parts of the Baltic; *Sardinella maderensis* is caught at sea with the stenohaline *S. aurita*, but it frequently enters estuaries and coastal lagoons (Longhurst 1971, p. 351: as *S. eba*); species of the Indo–Pacific anchovies *Thryssa* and *Setipinna* regularly enter brackish water, as do certain species of the New World

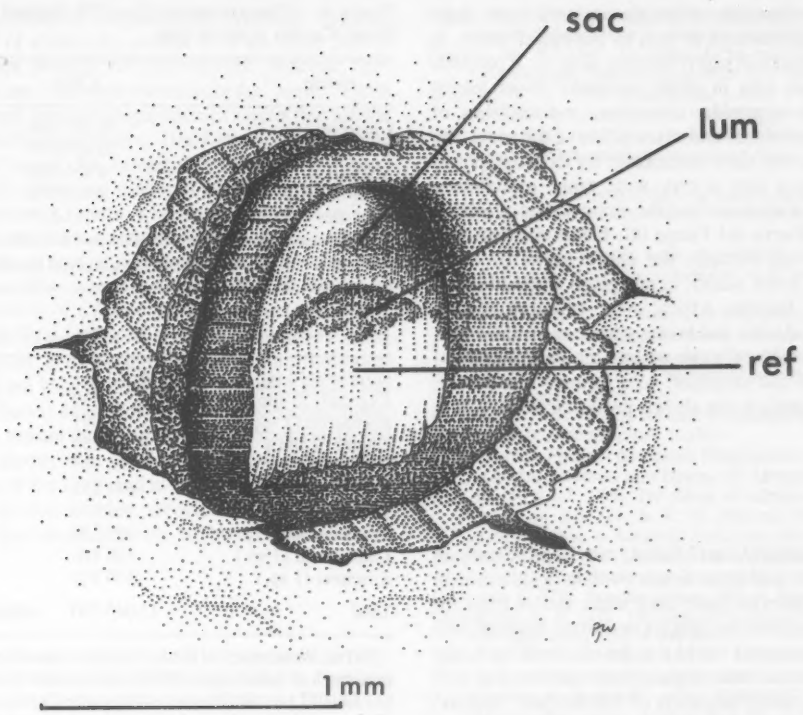

FIG. 16. Light organ of *Coilia dussumieri* showing sac containing luminous tissue (lum) and reflector (ref) below.

Anchoa and *Anchoviella*. Many species of shads (Alosinae) and gizzard shads (Dorosomatinae) have become fully anadromous, as also some species of the European clupeine *Clupeonella*; perhaps inevitably, some land-locked populations have arisen (Kilarney shad, *Alosa fallax killarnensis*; also *A. fallax lacustris* of Italian lakes). Other species have abandoned the seaward migration and are only found in rivers and lakes (the Australian *Nematalosa vlaminghi*, members of the Indian *Gonialosa* and *Gudusia*). Little trace of an anadromous ancestry remains in the West African pellonulines, almost all of which are totally freshwater (*Microthrissa*, *Cynothrissa*, *Potamothrissa*, etc.; also *Stolothrissa* and *Limnothrissa* of Lake Tanganyika); species of *Pellonula*, however, also occur in brackish water. In southern and western Africa it is largely the clupeids that have colonised freshwaters, but this probably reflects the fact that rather few engraulids occur off these coasts. In India, southeast Asia, and South America there are as many or more anchovies as herrings resident in freshwater. Unfortunately, records are not good and it is often impossible to judge if the species is anadromous or wholly confined to freshwater (unless caught far up the Amazon, Mekong, or other large river).

Many other aspects of clupeoid biology are also rather poorly known outside studies of the "classic" *Clupea* and *Engraulis* (and to a lesser extent *Sardina*, *Sardinops*, *Brevoortia*, etc.). For schooling, which seems to be a characteristic of at least the open-water clupeoids, Blaxter and Hunter (1982) cited laboratory studies on two species of the New World *Harengula* by Cullen et al. (1965), and Longhurst (1971) summarized data on the West African *Ethmalosa* and *Sardinella* (presumably *S. aurita*), as well as the New World *Opisthonema* and *Brevoortia*, but for the vast majority of warmwater clupeoids almost nothing is known of the size, shape, structure, and movement of schools (in the literature, that is, for the fishermen are often extremely observant of such things). Some clupeoids tend to abandon the tight school structure at night (Blaxter and Holliday 1963), and this has been very clearly documented for West African *Sardinella aurita* by Losse et al. (1971), who describe distinct scattering layers. Is this a general phenomenon of clupeoids? The same difficulties are encountered in breeding biology. *Clupea harengus* and *C. pallasi* (if distinct) are so far the only species known to deposit their eggs on the substrate (or on seaweeds). Is this true also of the South American *Clupea bentincki*, or were the small morphological differences that led to its placement in the subgenus *Strangomera* by Whitehead (1964) indicative of a quite different biology? Since only very rarely has the actual spawning of *Clupea harengus* been closely observed in situ (Aneer et al. 1983), it is perhaps not surprising that for most clupeoids only the grossest data are known: fecundity, general spawning season and area, a hint of migrations, approximate size, and age at first spawning (but considerable uncertainty whether the same fishes spawn twice in a year, what triggers spawning, why some year-classes are more successful than others, how eggs and larvae can be distinguished from those of closely related species, and many other facets of breeding that have been largely solved in the cool-water clupeoids). To some extent this reflects the difficulty of maintaining live clupeoids in poorly equipped laboratories. It is also the result of trying to study species that may school with one or more extremely similar congeners (e.g. *Sardinella*, *Stolephorus*, or *Thryssa* in the Indo–Pacific).

The diversity of clupeoids, although explored more thoroughly perhaps in morphological than in biological terms, is certainly impressive and will surely become more so. It parallels the kind of radiations seen in other successful lower teleost groups, such as the cyprinids, characins, and catfishes of freshwaters, or the stomioids and myctophids of the seas. The clupeoid radiation is even more remarkable for its geographical spread and penetration into a very wide range of habitats. Clupeoids are found in all seas, from the arctic waters of Siberia (*Clupea pallasi*) to Tierra del Fuego (*C. bentincki*) and New Zealand (*Sprattus*), off virtually the entire coasts of every continent and nearly every island, in numerous rivers of North and South America, Europe, Africa, Asia, and Australia, in inland seas (Caspian, Azov), and in many large and small lakes. In these waters they tolerate more or less the entire range of possible temperatures and salinities. As a formula for success, the basic clupeoid template has shown itself extremely adaptable.

Fisheries

Clupeoids are essentially "net" fishes, caught principally in beach seines, gill nets, and purse seines (with lamps), although traditional artisanal fisheries have used wiers and/or traps for catching migrating anadromous species or diurnal migrants into estuaries. Prior to the second world war the clupeoid catch was dominated by *Clupea* and other high-latitude species, but with the gradual postwar industrialization of low-latitude clupeoid fisheries (with the artisanal fisheries either left behind or themselves to some extent mechanized), it is now the tropical and subtropical clupeoids that predominate. As shown by Longhurst (1971, p. 349), the clupeoid catch grew at an annual 11.8% in the decade of the sixties, from 7.2×10^6 to 20.5×10^6 t (against a 6.3% growth for other sorts of fishes), and while the high-latitude clupeoid catches increased from 3.2×10^6 to 4.0×10^6 t, those of the low-latitude clupeoids increased fourfold, from 4.0×10^6 to 16×10^6 t. Admittedly, Longhurst's figures (based on FAO statistics) included the phenomenal rise of the Peruvian anchoveta fishery, which alone produced 2.9×10^6 to 10.3×10^6 t annually in this period, but there is no doubt that the low-latitude clupeoids have come to play an extremely important role in world fisheries, contributing in some areas as much as 20 or even 30% of the total catch. In fact, it is probably true to say that the clupeoids are the largest suborder of non-domesticated vertebrates harvested by man.

Clupeoid catch statistics for 1978 are shown in Table 4. In that year the clupeoids well exceeded the cod-like fishes and doubled the catch of the mackerels, tunas, and flatfishes combined. Marine clupeoids predominated, but freshwater and anadromous species (*Stolothrissa* and *Linothrissa* in Lake Tanganyika, *Tenualosa* (*Hilsa auct.*) of India) are clearly an important protein source in inland areas. Since the cool-water fisheries are for species monotypic in that area (or virtually so), it is not surprising that the top 10 clupeoid genera include only 20 species, of which almost all are from temperate waters. This tends to hide the importance of the multispecies tropical and subtropical clupeoids. Thus, *Sardinella* is seventh on the list when only the major species are included, but when all species of *Sardinella* are combined the catch is more than doubled and *Sardinella* is seen as one of the most important of genera and rivalling or exceeding *Clupea*. Noticeable also is the fact that the FAO fishery statistics, from whence these figures were drawn, lag far behind modern taxonomy because species are either misidentified or unidentified at source. Engraulids such as *Thryssa* or *Stolephorus* figure little or not at all in the statistics, yet their catch is considerable judging from markets in southeast Asia and India. The fishery for *Sardinella lemuru* off the Bali Strait and off western Australia is concealed by the names *S. longiceps* (of the Indian Ocean) or *Amblygaster posterus* (a supposed Australian endemic). An attempt to refine landing statistics is the production by FAO of species identification sheets for fishes of economic importance in various areas, especially in low latitudes.

TABLE 4. Clupeoid statistics for 1978 (derived from the FAO *Yearbook*). Catches in metric tons.

Group	Catch	% of all fishes
Clupeoids[a]	14 501 064	22.7
Cod-like fishes	10 450 295	16.3
Mackerels, etc.	4 056 928	6.3
Tuna-like fishes	2 522 332	3.9
Flatfishes	1 211 819	1.9

Top 20 marine clupeoid species

Genus	Catch	% of top 20	% of total clupeoids
Sardinops (4 spp.)	4 074 511	33.7	28.1
Engraulis (5 spp.)	2 726 898	22.6	18.8
Brevoortia (2 spp.)	1 177 091	9.7	8.1
Clupea (2 spp.)	1 102 159	9.1	7.6
Sardina (1 sp.)	800 935	6.6	5.5
Sprattus (1 sp.)	691 255	5.7	4.8
Sardinella (2 spp.)	563 946	4.7	3.9
Opisthonema (1 sp.)	403 254	3.3	2.8
Clupeonella (1 sp.)	396 106	3.3	2.7
Etrumeus (1 sp.)	109 515	1.0	0.8
Total	12 045 670	—	83.1[b]

NOTE: World catch of fishes, marine mammals, etc. = 72 379 500 t; total catch of fishes only = 63 957 487 t. Half the world catch of fishes (33 590 027 t or 52.5%) came from only 63 fish species, of which 20 of these (35.9% of the catch) comprised clupeoids.

[a]Marine clupeoids = 13 915 017 t; freshwater, anadromous clupeoids = 586 047 t.

[b]Or 18.8% of the total world catch (all groups).

As pointed out by Blaxter and Hunter (1982, p. 164), clupeoid stocks seem not to have strong density-dependent regulatory mechanisms, with the result that recruitment and population size can show extreme natural variability; as a concomitant, clupeoid stocks are highly susceptible to overfishing (Cushing 1971). In a sense, this probably cuts both ways. The decline of certain clupeoid stocks (*Clupea*, *Sardinops*, anchoveta) is the result of both overfishing and natural changes, but by the same token, recovery of the stocks is also possible. It is by no means certain, however, that this can be extrapolated to the multispecies tropical clupeoid fisheries and is certainly no excuse for *laissez faire* fishery policies. Rational exploitation of tropical clupeoid stocks requires far more biological knowledge than we have at the moment.

Conclusion

Time and again in the *Clupea* literature it seems taken for

granted that the attributes of *Clupea* are in some way "typical" or "characteristic" of clupeoids, almost as if the other 300 or so clupeoids (except perhaps the high-latitude *Sardina*, *Sardinops*, *Engraulis*, etc.) are aberrations from the "norm." Quite possibly it is the high-latitude single-species stocks that are the later variants on the clupeoid theme. Had Linnaeus, Bloch, and Lacepède, as well as all the subsequent *Clupea* specialists, worked in the real centres of clupeoid diversity, say in the Caribbean or Indonesia, quite a different concept of the "typical" clupeoid would have emerged. Historical "accidents" do indeed shape the course of research, both in the selection of problems and in their interpretation. One good reason to apply the sophistication of *Clupea* research to the warm-water clupeoids, therefore, is that this will provide a broader context to high-latitude studies, at the least by showing which biological or other attributes are basic to the whole clupeoid group and which must be reckoned adaptations to cool-water conditions. The second good reason to bring northern expertise to the tropical stocks is simply that the latter are now rivalling the traditional fisheries of the north and at the same time are in those very areas where protein is most needed. In a century or so, King Herring may have lost his crown, but he will surely be held as a pioneer.

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The Herring: A Successful Species?[1]

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The herring has an elaborate racial system closely linked to its spawning habits. Its demersal eggs are laid in a wide range of environments from the deeper parts of the continental shelf to the intertidal zone and in a wide range of salinities and temperatures between latitudes 35 and 70°N. Depending on the race, spawning occurs in all months of the year and the relationship between fecundity and egg size is correlated with the season, with high fecundity and small eggs in the summer and fall and low fecundity and large eggs in the winter and spring. The herring is specially adapted in other respects. There is a complex camouflage system based on silvery layers of guanine crystals in the skin, a specialised retina, and a very complex acoustico–lateralis system linked to the swimbladder. It is physostomous, allowing rapid vertical movements of wide amplitude, and strongly schooling in habit with the facility to switch from particulate to filter-feeding. Filter-feeding can continue in darkness. Although many herring stocks have been overfished, there is no reason to suppose that they cannot recover, to the historical high levels, if properly managed. The stock size varies from millions to hundreds of tonnes, depending on the race, and this has interesting implications for the stock–recruitment relationship.

On observe chez le hareng un système racial élaboré qui est étroitement lié au cycle de reproduction. Les œufs sont pondus au fond de l'eau, dans une grande variété de milieux, depuis les plus grandes profondeurs de la plate-forme continentale jusqu'à la zone intertidale, dans des eaux dont la salinité et la température varient considérablement entre 35 et 70° de latitude N. La période de frai dépend de la race ; il y en a toute l'année et la relation entre la fécondité et la taille des œufs est en corrélation avec la saison ; ainsi, la fécondité est élevée et les œufs sont petits en été et en automne, tandis que la fécondité est faible et les œufs sont gros en hiver et au printemps. Le hareng présente des adaptations particulières à d'autres points de vue. En effet, il est pourvu d'un système de camouflage complexe, une couche argentée de cristaux de guanine dans la peau, d'une rétine spécialisée et d'un système acoustico–latéral fort complexe qui est relié à la vessie natatoire. Comme il est physostome, il peut effectuer de rapides mouvements verticaux de grande amplitude ; il est aussi très grégaire et peut facilement passer d'un mode d'alimentation à base de particules à un mode d'alimentation par filtration, ce dernier pouvant se poursuivre la nuit. Bien des stocks ont été surexploités, mais il n'y a aucune raison de croire qu'ils ne puissent être ramenés aux anciens niveaux s'ils sont bien gérés. Un stock représente des millions ou des centaines de tonnes selon la race ; c'est là un fait intéressant à considérer dans l'étude des relations entre l'importance des stocks et le recrutement.

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Success may be defined in terms of worldwide biomass, population numbers, the ability to adapt to environmental change, or to rectify population decline. Historically, the herring has played a major economic role in the development of European coastal ports from the times of the Hanseatic league in the Middle Ages up to the present century where it has been one of the mainstays of fishing ports of Northwest Europe. This is less true of the smaller herring stocks of the Northeast Atlantic and Northwest Pacific.

Apart from establishing the present role of the herring as a fish of world importance and its potential as a resource for the future, the aim of this paper will be to discuss those features of herring biology that may account for its success and especially its ability to reproduce in a very wide range of environments.

Biomass

Landings of Atlantic herring (*Clupea harengus harengus*) have always substantially exceeded those of Pacific herring (*Clupea harengus pallasi*) by a factor of 2–8 (Fig. 1). At their best in the mid-1960's the total catch of both groups was over 4.5 million tonnes, or about 11.5% of the world marine fin fish catch. Only the Peruvian anchoveta (*Engraulis ringens*), at its peak, has exceeded this total. Subsequent overfishing led to complete closures of several herring fisheries in Northeast European waters in the mid- to late 1970's. There have since been signs of a slow recovery, and limited fishing has been reintroduced (see Jakobsson 1985).

In terms of biomass the herring has historically been

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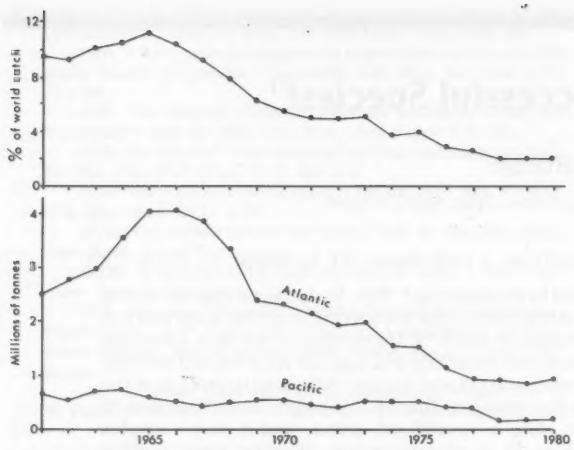

FIG. 1. Weight of Atlantic and Pacific herring landed from 1961 to 1980. Top panel: both stocks as a percentage of the total world marine fin fish catch; bottom panel: in terms of weight for the two stocks separately. (From F.A.O. Year Books of Fishery Statistics)

extremely successful. Some of the reasons for the catastrophic decline and the failure of scientists and administrators to prevent it will emerge later in this paper.

Distribution

Let us now examine some of the factors that may determine the potentially high biomass of the herring. The worldwide distribution taken from Svetovidov's (1963) monograph is shown in Fig. 2. Following the Russian custom, herring are divided into five subspecies: (1) *Clupea harengus harengus* (North Atlantic and Barents seas), (2) *Clupea harengus membras* (Baltic Sea), (3) *Clupea harengus pallasii* (Pacific, Arctic, and adjoining seas), (4) *Clupea harengus pallasii maris-albi* (White Sea area), and (5) *Clupea harengus pallasii suworowi* (Chesha Bay area). These subspecies are delimited mainly geographically but they have differences in meristic characters, especially of the vertebral counts, and of the body dimensions and the size at first maturity and asymptotic length. This differentiation of herring stocks will be discussed later.

For our purposes the divisions of Svetovidov (1963) will be used as convenient descriptive terms but without a detailed analysis of the systematic implications. As far as management of the fisheries is concerned the issue is unimportant. Blaxter (1958), however, considered that Atlantic and Pacific stocks of herring were sufficiently different to be categorised as valid species, and N. Ryman (pers. comm.) reported that recent electrophoretic studies confirm this view. Kornfield et al. (1982), using starch gel electrophoresis, found highly significant genetic heterogeneity between spring and fall stocks of Atlantic herring on the east coast of Canada. There seems to be a strong likelihood that further speciation is in progress in many herring stocks. The characteristics of herring that may contribute to its success are listed in Table 1.

TABLE 1. Special features of herring.

Reproduction
Widely distributed spawning grounds
Year-round spawning
Wide range of fecundity and egg size
Demersal eggs
Large larvae
Race
Complex racial system linked to reproduction
Physiology
Euryhaline
Guanine reflecting layers
Specialised eye
Physostomous
Complex auditory system
Head lateral line only
Behaviour
Schooling
Particulate and filter-feeding modes
Vertical migration
Stock size
Varying from millions to hundreds (?) of tonnes

Reproduction

Atlantic herring lay demersal eggs usually on offshore gravel banks in depths of 5–150 m. Pacific herring lay their eggs intertidally or sublittorally on seaweed and eelgrass. The spawning grounds have been fully investigated and are shown together with some of their characteristics in Fig. 3. The latitude for spawning ranges from about 35 to 70°N and depends on the temperature conditions, so that spawning is generally early in low latitudes and later in high latitudes. Spawning, however, takes place (in one group or another) in all months of the year, and the range of environmental conditions in which spawning is apparently possible is remarkable. It extends from salinities of 2‰ or less in the Baltic to oceanic salinities of 34–35‰ on the open sea grounds. Although ranges of temperature for spawning are to some extent reduced by the choice of spawning season, it seems that spawning can take place over a wide range, for example, in the McKenzie river in northern Canada under the ice (Kristofferson, unpubl.), in the White Sea at temperatures below 0°C, and up to 13–15°C in other areas. At high latitudes, temperatures can rise very fast during incubation. Pacific herring can withstand, at least for a short time, extremes of temperature when the tide ebbs as well as, presumably, a degree of desiccation. This eurythermy, together with euryhalinity, means that the herring egg has a formidable ability to survive in harsh environments.

The herring has evolved, by marine fish standards, a fairly large egg (and therefore a large newly hatched larva) and a quite remarkable range of adaptations to spawning in different seasons in terms of the interplay between egg size and fecundity. Figure 4 shows, for selected spawning groups, how winter–spring spawners have large eggs and low fecundity, while summer–fall spawners have small eggs and high fecundity. It is thought (Hempel and Blaxter 1967) that large eggs and low fecundity are of advantage in poor larval food/low predator density conditions and small eggs and high fecundity have greater adaptive value in conditions of a good larval food supply and high predator density.

Although Lambert (1984) reported pulses of spawning on a ground in the Southern Gulf of St. Lawrence, it is more common for spawning to occur over a period of a few weeks on any given ground. This one-off, fixed annual spawning pattern is, however, coupled with great flexibility in terms of resistance to environmental conditions and in terms of adaptation to an optimum egg size–fecundity relationship.

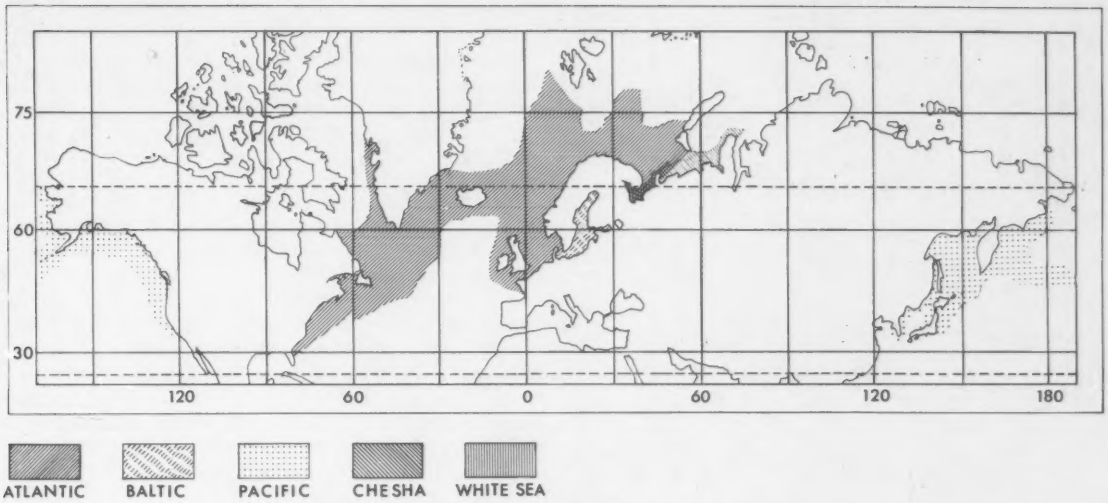

FIG. 2. Geographical distribution of herring divided into five main subgroups. (Redrawn from Svetovidov 1963)

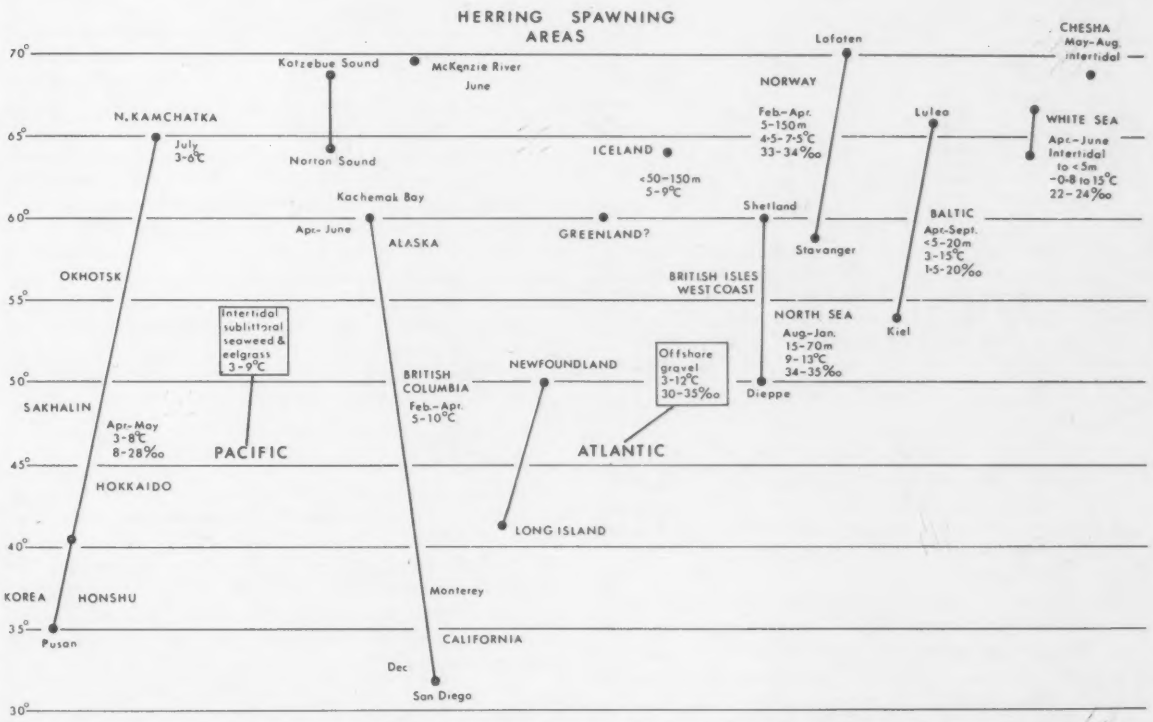

FIG. 3. Main spawning areas of herring in relation to latitude. Some details of environmental conditions are given. (Data from Alderdice and Velsen 1971; G. Aneer, pers. comm.; Dragesund 1970; Einarsson 1956; Galkina 1971; Hay 1985; Motoda and Hirano 1963; Rounsefell 1929; Runnström 1941; Soin 1971; Svetovidov 1963; Taylor 1971)

Race

The earlier work by Heincke (1898), followed by later work of herring biologists such as Schnakenbeck (1927), Lissner (1934), Cushing (1955), Blaxter (1958), Svetovidov (1963), and Zijlstra (1969), has shown a great complexity of racial makeup, especially in Atlantic herring. The evidence (e.g. Jones 1968; Zijlstra 1969) suggests that the characters examined are fairly stable. While there may be some interchange, in that fish hatched on a particular ground may not return to it to spawn (Burd 1962), most mature fish probably return within their own lifetime to the same spawning ground year after year. It is not

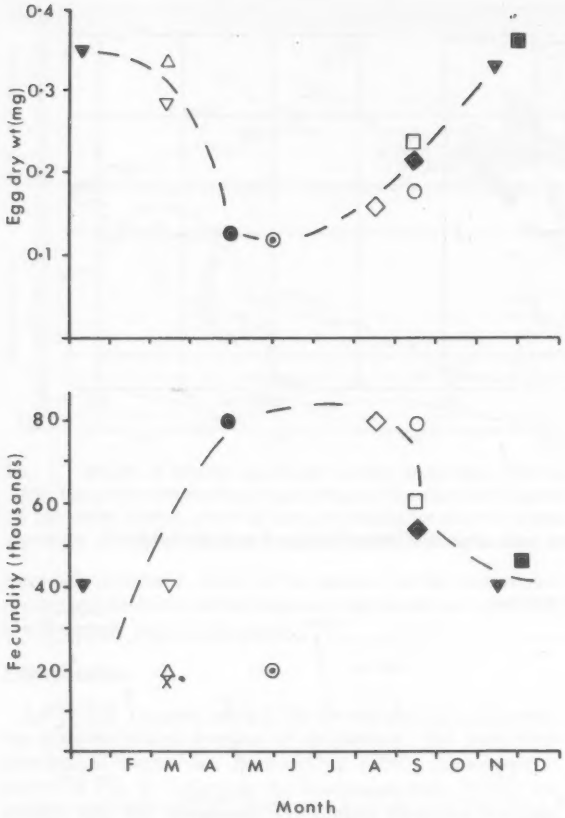

FIG. 4. Relationship between egg dry weight and fecundity in herring spawning at different seasons. Fecundity data are for 28-cm-long fish except for the eastern Baltic (18 cm) and British Columbia (20 cm). ▼, S. Irish; ▽, Clyde; △, Norway; X, British Columbia; ●, W. Baltic; ⊙, E. Baltic; ◇, N. North Sea; □, Isle of Man; ◆, Central North Sea; ○, Minch; ■, S. North Sea. (Data from Anokhina 1971; Kändler and Dutt 1958; Hempel and Blaxter 1967; Nagasaki 1958; Parrish and Saville 1965)

clear, then, how complete or effective reproductive isolation is. It is quite likely that it is not significant within, for example, the North Sea summer–autumn spawners, although it is likely to be significant when comparing, for example, North Sea, Baltic, and Norwegian stocks.

Some idea of the combination of characters used and their range of values is shown in Table 2, using four examples. A number of points emerge. First, racial makeup and spawning characteristics are closely related. In a sense, the spawning flexibility of herring results from the racial system, which has both an anatomical and a physiological basis. Second, the four examples taken are groups that are widely different. Other, more closely related groups with smaller differences in the characteristics could have been chosen. Third, many racial analyses require a sample of fish to be taken and a mean value (e.g. of vertebral count or keeled scale count) to be calculated. Many racial characters do not allow an *individual* fish to be assigned to its race. Racial analysis is the key to separation of stocks of herring and to the estimation of fishing intensity on different stocks in periods of the life history when they are mixed.

Physiology

A study of the herring shows it to have a number of special adaptations that increase its ability to colonise different environments, avoid predators, and locate food.

Euryhalinity

The effect of different salinities on fertilization, hatching, and larval and adult survival is shown in Fig. 5. The optimum for Pacific herring (about 20‰, Alderdice and Velsen 1971) is less than that for Atlantic herring. The herring is very tolerant of salinities far below the osmotic pressure of the body fluids (equivalent to 12–16‰ salinity). While the resistance to salinities above 35‰ seems to be valueless (unless under desiccation), the wide tolerance is a sign of efficient osmoregulation and of an ability to survive low-salinity environments. This must be the main key to the wide distribution of the herring generally and of its spawning grounds in particular.

Guanine Reflecting Layers

It was first realised by Denton and Nicol (1965) that the silvery-sided nature of the herring flank was a subtle adaptation for camouflage. The guanine reflecting platelets lie under the scales in such a way that they act as vertical or near-vertical mirrors. A high degree of reflectivity is produced by constructive interference from several such layers. The effect is that of the whole flank acting as a mirror and so matching the background light when viewed from the side. The dorsum is black, which helps to match the minimal upwelling light when viewed from above, and the ventral surface has a slim keel that reduces the silhouette effect when viewed from below. This excellent camouflage system will tend to make herring inconspicuous to predators, but it will also make it more difficult for the fish to use vision for station-keeping in the school. The maximum camouflage effect is only obtained when the distribution of light downwelling from the surface is homogeneous from all azimuths. This will be least true at dusk and dawn (when the sun is near the horizon). The school will then find it easier to use vision to retain contact at dusk and to resume contact at dawn.

Specialised Eye

The herring retina has a specialised ventro–posterior region known as the "area temporalis" (Blaxter and Jones 1967). The area is packed with a slim type of cone and few rods are present. The improvement in acuity (Fig. 6) gives a visual axis in the upper-fore direction. Herring normally feed on particles by approaching them from slightly below and it seems likely that they are using this part of the retina for visual tasks where high acuity is desirable.

Physostomy

All the clupeoids are physostomous. The herring not only has a pneumatic duct leading from the posterior end of the stomach to the swimbladder but an anal duct as well. It is generally accepted (Blaxter et al. 1979) that the herring swimbladder plays a minor role in buoyancy and that it functions mainly as a reservoir for the acoustic system (Fig. 7). The lack of a buoyancy function must be set against the advantages of making rapid upward movements in response to predators or as part of the diel vertical migration cycle. This is not possible in

TABLE 2. Some racial characteristics of four spawning subgroups of herring according to geographic location. Other characteristics that have been counted include lateral fin rays, median fin rays, scales, gill rakers. Data taken from Anokhina (1971), Baxter (1959), Beverton (1963), Burd (1962), Kingston (1982), Marty (1959), Nagasaki (1958), Parrish and Saville (1965), Popiel (1958), Schnakenbeck (1927), and Tester (1937).

Characteristic	Norway	Northern North Sea	Southeastern Baltic	British Columbia
Spawning time	Mar.–Apr.	Aug.–Sept.	Apr.–May	Feb.–Apr.
Substratum, depth	Gravel, 5–150 m	Gravel, 15–70 m	Gravel, sublittoral	Weed, intertidal and sublittoral
Fecundity range (thousands)	40–80	40–120	8–25	8–36
Egg dry weight range (mg)	0.2–0.45	0.11–0.20	0.08–0.18	0.15–0.33
l_1 (cm)	7–10	13.5–15.2	6–10	7.4–8.7
l_m (cm)	28–29	24–25	14–15	21–22
l_∞ (cm)	35–37	31–32	27–28	27–28
Maximum age (yr)	19–23	15–16	11–12	11–12
Growth coefficient (k)	0.17–0.25	0.35–0.43	0.55–0.60	0.40–0.55
Mean vertebral count	56.9–57.6	56.4–56.6	55.2–55.6	53.7–54.4
Keeled scales (K_2)	13.3–14.5	13.8–14.5	14.0–14.5	11.8–12.1

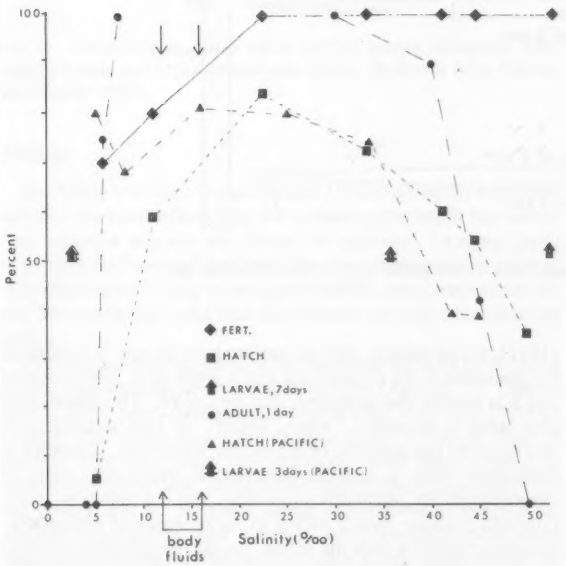

FIG. 5. Euryhalinity of Atlantic herring (except where stated in the key) from Holliday and Blaxter (1960, 1961), Alderdice and Velsen (1971), and Alderdice et al. (1979). Heavy arrows for newly hatched larvae show the lowest and highest salinity giving 50% survival over 3 d (Pacific herring) and 7 d (Atlantic herring). Survival of adults is given at different salinities over 24 h.

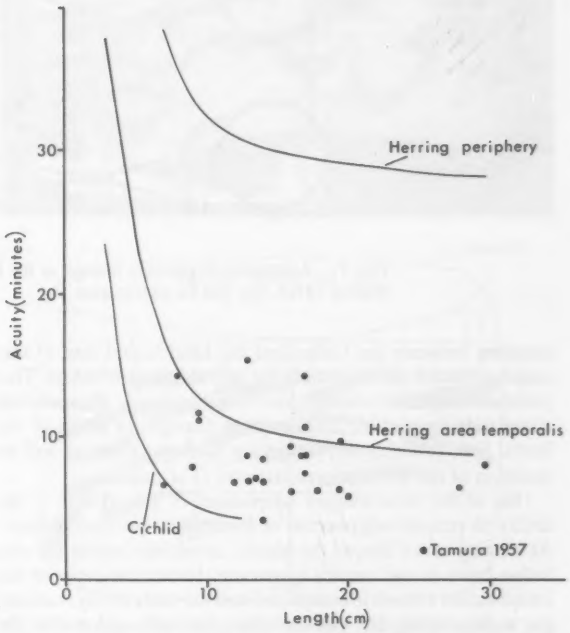

FIG. 6. Acuity (as minimum separable angle) in relation to body length in the herring area temporalis compared with the peripheral retina (from Blaxter and Jones 1967). The acuity of a Cichlid *Aequidens portalegrensis* (Baerends et al. 1960) and for 26 different species of teleost (Tamura 1957) is given for comparison.

physoclistous fish, which could burst the swimbladder during a rapid ascent.

Acoustico–Lateralis System

A substantial body of work exists on the acoustico–lateralis system of the clupeoids. Much of the work on herring is summarized by Allen et al. (1976), Denton and Blaxter (1976), and Blaxter et al. (1981a).

It is not intended to repeat here the detailed workings of this system. Suffice it to say that the otic bullae, which contain gas constrained by an elastic membrane, act as localised amplifiers of sound pressure within the skull, close to the labyrinth of the inner ear. This endows the herring with excellent hearing sensitivity and a wide frequency range so that it compares favourably with ostariophysine fish (Fig. 8). There is a unique

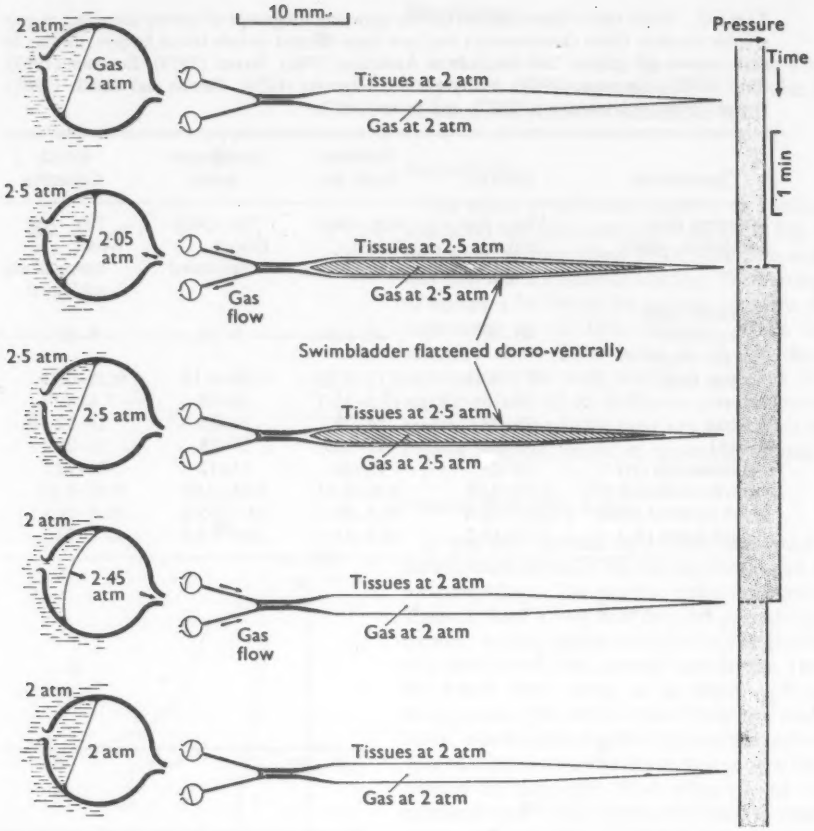

FIG. 7. Adaptation to pressure change in the herring bulla–swimbladder system (from Denton and Blaxter 1976). See text for explanation.

coupling between the bullae and the head lateral line so that sound pressures also stimulate the lateral line neuromasts. This internal source of stimulation, together with the external stimulation by particle displacement through the pores of the lateral line, probably allows herring to detect range as well as direction of the sound source (Blaxter et al. 1981a).

One of the most elegant adaptations of this system is the ability to remain independent of hydrostatic pressure change. As herring move deeper the elastic membrane within the otic bullae bows in and creates a pressure differential between the swimbladder (which is compliant) and the bulla cavity, causing gas to flow along fine gas ducts into the bulla and restore the membrane to a flat position (Fig. 7). Movement upwards decreases the hydrostatic pressure, causes the membrane to bow out, and gas flows back to the swimbladder. This mechanism keeps the membrane flat during depth changes, the position in which the membrane is most sensitive. It also prevents the membrane from bursting. Thus, hearing is not impaired during the diel vertical migration cycle.

Behaviour

Schooling

The role of schooling, fully discussed by Blaxter and Hunter (1982), seems mainly to be an antipredator device. It is difficult for predators to fix on and pick out a single prey from a school and it is usually the stragglers that are caught. The school may also have a so-called "sentry effect" in that awareness is increased by the presence of many fish. Generally, schooling is associated with a limited behavioural repertoire, lack of manoeuvrability, difficulty in taming, and the ability to maintain high cruising speeds owing to the presence of red muscle. Interfish contact within the school seems remarkable, with few signs of collisions taking place, and it seems likely that interfish distance is a balance between attraction by vision and repulsion by lateral line stimuli.

The herring displays a well-marked "Mauthner" response: a sharp turn after receiving mechanical stimuli with a latency of 20–30 ms (Blaxter et al. 1981b). The turn is usually directed away from the sound source (Fig. 9) and the fish only requires about one cycle of sound to obtain sufficient information to make the turn directional. The sensitivity of herring to such stimuli is mainly due to the presence of the otic bullae, and if the elastic bulla membrane is burst the sensitivity drops by about 10 times (Blaxter and Hoss 1981).

It seems likely that the acoustico–lateralis system of herring, giving the ability to respond to transients directionally, is an adaptation that enhances the cohesiveness of a school and improves the ability to avoid predators.

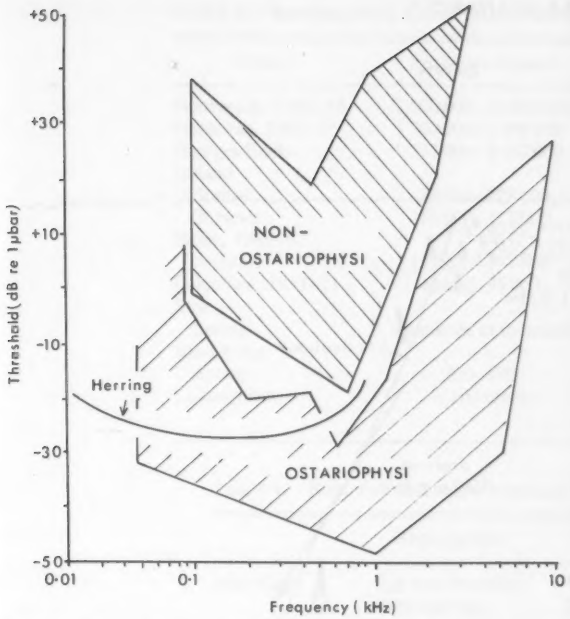

FIG. 8. Frequency response curve for the herring compared with ostariophysine and nonostariophysine fishes. (Redrawn from Blaxter and Hunter 1982)

Feeding

It is likely (see Blaxter and Hunter 1982) that tightly knit large schools are most efficacious for reducing predation but small, less cohesive schools are better for optimum foraging (both searching for food and feeding). Smaller, less cohesive schools will mean less overlap of perceptive fields, less competition for the food available, and less interference in individual feeding acts.

Particulate feeding seems to be mediated visually by the high acuity area temporalis, but recent work at Oban (R. N. Gibson and I. Ezzi, pers. comm.) has shown that adult and juvenile herring can switch to a filter-feeding mode if offered food of particle size less than 300–400 μm. This filter-feeding is maintained in the dark, as shown by unpublished experiments of the author and R. S. Batty using infrared/video techniques. Earlier conclusions that herring were daylight particulate feeders must therefore be revised, with all the implications for herring energetics.

Vertical Migration

The diel activity rhythms of herring in some ways epitomise the species and its special characteristics. Herring, at least as adults, spend the daylight hours in schools near the seabed. At dusk they move towards the surface following a light preferendum of about 1 lx (Fig. 10). The upward migration rate in terms of rate of pressure decrease is far higher than would be possible for a physoclistous fish. Feeding activity seems to increase as the fish near the surface, and as the light decreases, further visual attraction within the school ceases and the fish disperse to form a scattering layer. It seems likely that herring can switch to filter-feeding during the night if the particle size of the food present is suitable. At dawn the school reforms as the light

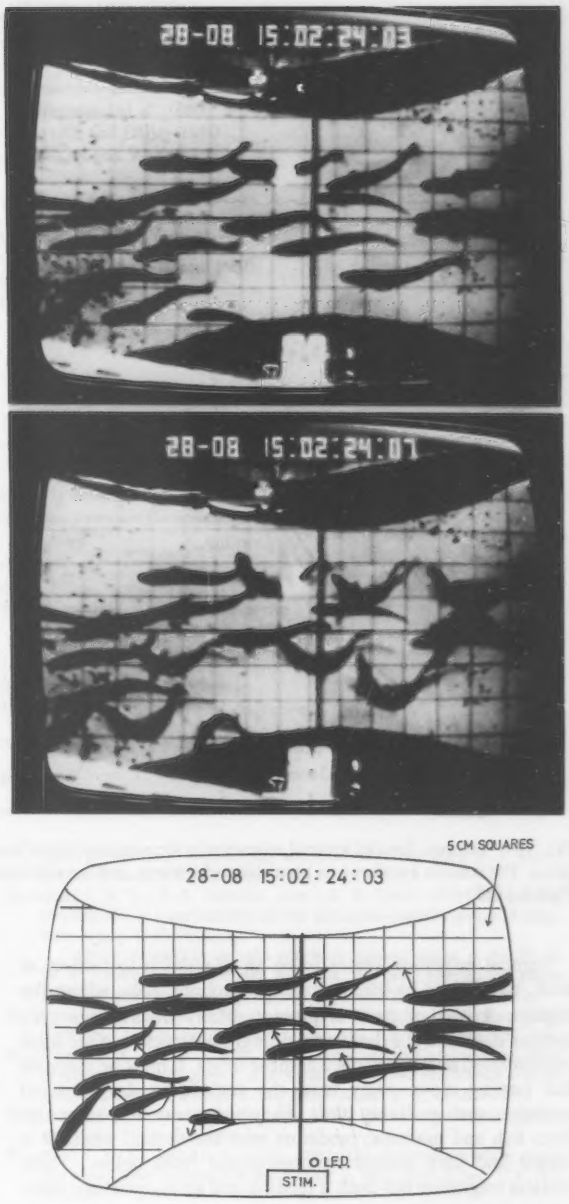

FIG. 9. Frames from video film showing the startle response in a herring school swimming between netting "islands" in a tank. Top panel: the school just before a sound stimulus; middle panel: the school 40 ms after the stimulus (note that many fish turn away from the source, which is located at the lower edge of the frames); bottom panel: composite diagram of the two frames with arrows showing the movement of the fish. Stim., stimulus source; LED, light-emitting diode (which gives timing of stimulus). (From Blaxter et al. 1981b)

intensity increases above the schooling threshold. The silvery-sided effect is least effective at this time, so enhancing the visibility of the fish to each other. Particulate feeding may recommence as the fish begin to "follow the light preferendum" into deeper water.

FIG. 10. Scenario for diel vertical migration in the northern North Sea. An isolux line and typical rates of decompression and compression are given. The schools are shown as plumelike echo traces, and the nighttime scattering layer shows the fish dispersed near the surface. (Blaxter and Parrish 1965)

Vertical migration seems to be an adaptation to feeding at dusk, dawn, and in the dark in the euphotic zone where the highest density of food is present. Many invertebrate prey species also follow a diel vertical migration cycle and are most concentrated near the surface at these times. It must be assumed that herring move away from the surface by day to avoid predators such as diving birds. They are presumably safer also from fish and mammal predators near the seabed where it is darker and they cannot be approached from below. Thus, vertical migration has both a feeding and an antipredator role.

Stock Size

Finally, it may be useful to look at the stock sizes of herring. Recent work using virtual population analysis (VPA), tagging, egg and larval surveys, and acoustical techniques has made estimates possible. Some data using VPA (Table 3) demonstrate the variation in stock size (at a time when overfishing does not appear to have been significant) from millions of tonnes in some of the big offshore stocks, to tens of thousands in more inshore stocks, such as the Baltic, to perhaps only hundreds or thousands of tonnes in small estuarine stocks. Apparently, some special features of the stock–recruitment relationship allow small stocks to be self-maintaining at levels far below what would be viable for larger offshore stocks. These special features are not understood although it seems likely that small stocks do not make large-scale migrations and their spawning grounds are very limited in area.

By way of summary, Table 4 has been drawn up to show the characteristics of herring discussed in this paper in terms of the role they play in its life history. Three categories may be identified, reproductive, feeding, and antipredator, and each may operate at the individual, interfish, or species level. It is the reproductive adaptations and the racial structure of the species that allow the wide colonisation of environments and presumably the flexibility of the stock–recruitment relationships discussed above. Feeding and predator avoidance are closely linked to the vertical migration cycle, with schooling as a vital component. It is the latter that has probably led to the catastrophic reduction of so many stocks. The "classic" signs of overfishing are a decline in the catch per unit of effort (CPUE) and a reduction in the numbers of larger fish. In an overfished herring stock the CPUE does not necessarily fall initially, since the surviving herring aggregate by schooling and the searching power of the fishing fleet allows the fishermen to seek out these survivors on a contracted fishing ground. The growth characteristics of herring are such that recruit overfishing does not cause the same dramatic loss of larger fish as is found, for instance, in

TABLE 3. Spawning stock size of various herring groups without signs of major overfishing.

Group	Spawners (tonnes)	Reference
Norwegian, 1950–66	2 500 000–10 000 000	Dragesund et al. 1980
North Sea, 1947–65	1 700 000–3 300 000	Saville and Bailey 1980
Georges Bank	272 000–1 140 000	Antony and Waring 1980
Iceland		
Spring	73 000–778 000	Jakobsson 1980
Summer	56 000–313 000	
Baltic, 1966–67		
Autumn	127 000–147 000	Rechlin and Borrmann 1980
Celtic Sea, 1957–71	40 000–95 000	Molloy 1980
Elbe		
Spring	Hundreds to thousands?	Estimate by author
Blackwater		
Spring	200–800	Wood 1981
Lindaspollen	<100 tonnes	A. Johannessen, Dept. of Fisheries Biology, Bergen University, pers. comm.

TABLE 4. Role of various characteristics as they apply to different aspects of herring life.

	Reproductive	Feeding	Antipredator
Individual	Egg size/fecundity Demersal egg Euryhalinity Large larva.	Vision Switching modes	Vision Startle response Camouflage (guanine) Physostomy
Interfish	Spawning ground and season	Vertical migration Schooling (?)	Schooling Vertical migration
Implications for species	Racial system Colonisation Stock size	Feeding versatility	Exploitation by man

gadoid species. Hence, scientists have had little warning and little time to act to remedy a deteriorating situation. After the closure of several fisheries and their reopening under tighter control, there are signs of the stocks building up again. It seems likely that the herring will prove to be a successful species in terms of its ability to recover from drastic overfishing.

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What Limits Clupeoid Production?[1]

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Lasker, R. 1985. What limits clupeoid production? Can. J. Fish. Aquat. Sci. 42 (Suppl. 1): 31–38.

This review paper explores a number of hypotheses on the control of clupeoid populations. The following are discussed: the effect of fishing; egg mortality (predation); larval mortality (the critical period) with a consideration of starvation and predation and the biotic and abiotic factors that may be involved; larval transport and the oceanographic features that cause it; variable egg production; interspecific competition; and the effect of localized (e.g. storms and upwellings) and widespread (El Niño) oceanographic events. A review of the paleosedimentary record is also given showing the magnitude of natural fluctuations when no fishing occurred. Recent resurgences in clupeoid populations are reviewed and suggested causes are analyzed.

Le document aborde un certain nombre d'hypothèses concernant le contrôle des populations de clupéidés. Il y est question entre autres des conséquences de la pêche, du taux de mortalité parmi les oeufs (activité des prédateurs), de la mortalité des larves (période critique) de sous-alimentation, des prédateurs, des facteurs biotiques et abiotiques qui peuvent entrer en ligne de compte, du transport des larves et des facteurs océanographiques connexes, des variations au niveau de la production des oeufs, de la lutte entre les espèces, de même que des conséquences de certains faits océanographiques localisés (tempêtes, remontées d'eau, etc) et plus étendus (courant El Niño). L'auteur traite également des facteurs paléosédimentaires, illustrant l'amplitude des fluctuations normales en l'absence d'exploitation commerciale. Le document étudie enfin les réapparitions récentes de populations de clupéidés et analyse les causes qui expliqueraient pareils phénomèmes.

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Research devoted to the subject of recruitment mechanisms has been growing in the last few years. The fluctuations in populations of clupeoids in particular have given impetus to these investigations because of the great economic and food value of these fishes. For example, anchovy and menhaden fish meal are used as a protein source in poultry and cattle feed, and sardines, herring, anchovy, and a variety of other clupeoids are used directly for human food. In all, clupeoids make up about 30% of the 70 million metric ton (t) world fish catch alone. The importance to individual nations is exemplified by the fishery for the Peruvian anchoveta, *Engraulis ringens*, which at its height accounted for over 12 million t/yr or 15% of the world fish catch. The rise and fall of this great fishery and the economic changes that occurred in the fishmeal and soybean markets when fishmeal became scarce and a protein substitute was needed are shown in Fig. 1a. A number of other examples of the rise and fall (Murphy 1977) and sometimes rise again of specific clupeoid fisheries are available, e.g. the sardine fishery in Japan (Kondo 1980), the herring fishery in the North Sea (Hempel 1978), the Peruvian–Chilean sardine (Lasker and MacCall 1983) and anchoveta (Barber et al. 1980), and the Pacific sardine off California (Marr 1960). My paper reviews a number of hypotheses on the control of clupeoid populations.

The Paleosedimentary Record

There is little question today that there are natural fluctuations of great magnitude in fish populations which are attributable to causes other than fishing. The best evidence for naturally occurring increases and declines is from the sedimentary record of anaerobic basins. For example, Soutar and Isaacs (1969) reconstructed the population fluctuations of some of the common fishes occurring off California by identifying and counting fish scales in cores taken from anaerobic sediments of the Santa Barbara Basin. The Pacific sardine, *Sardinops sagax* (also *S. caerulea*), was greatly abundant about 1000 yr ago, much more so than in the recent history of the fishery when peak biomass was estimated to be only about 2 million t. Similarly, the northern anchovy, *Engraulis mordax*, while always abundant, also declined in biomass from 1600 yr ago to the present. Of greater interest, perhaps, is the 19th and 20th century history of anchovy and sardine fluctuations which was presented in a later paper by Soutar and Isaacs (1974). They showed that the modern decline of the Pacific sardine started about 1890, 30 yr before the inception of a fishery off the west coast of the United States. Exceptional year classes could be seen as having occurred in 1855 and 1865, yet these were not sufficient to prevent "a precipitous and natural decline" in the 1870s. In considering the paleosedimentary record, Lasker and MacCall

[1]This paper was presented at the International Symposium on the Biological Characteristics of Herring and Their Implication for Management, convened at Nanaimo, B.C., June 20–22, 1983, commemorating the 75th anniversary of the Pacific Biological Station.

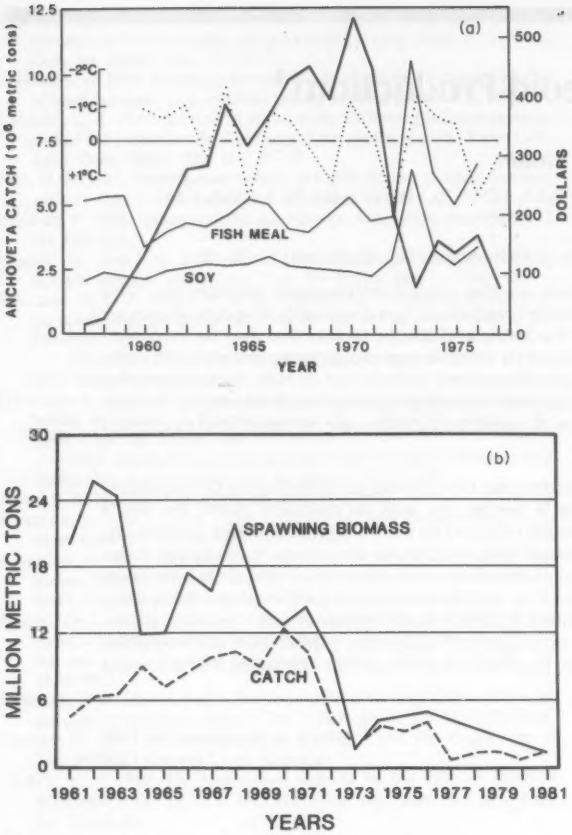

FIG. 1 (a) Peruvian anchoveta catch from 1957 to 1977. The temperature anomaly around a 19-yr mean of 23.8°C is shown with a dotted line. The El Niño of 1972 corresponds with a sharp decrease in catch. This is discussed in the text. Fish meal and soybean prices are plotted to indicate the possible effect of the diminished Peruvian anchoveta catch on the world protein market (after Barber et al. 1980). (b) Peruvian anchoveta catch from 1961 through 1981 compared with the spawning biomass (after Csirke 1980; Tsukayama 1982).

(1983) concluded that the Soutar and Isaacs (1969, 1974) data were probably too insensitive to detect below 500 000 to 1 million t sardine biomasses. The most recent (1983) biomass figures put the Pacific sardine in California waters at less than 20 000 t (Klingbeil 1983). Thus, the decline of the sardine in the 1870s and 1890s was not the same phenomenon as that which occurred off California in the 1940s. The latter was undoubtedly much more drastic and obviously had a component of heavy exploitation which appeared to force the population below its minimum spawning stock size.

Following the recent sardine population decline, there was an increase in the anchovy population off California (Huppert et al. 1980), but the anchovy was also at much higher population levels in the late 19th and early 20th centuries. In comparison, off Peru, DeVries and Pearcy (1982), using the techniques of Soutar and Isaacs, showed that the clupeoid biomass off Peru has also fluctuated greatly; the stocks of anchoveta and sardine were not as abundant in the late Pleistocene (11 000 yr ago) as they have been in recent times.

The Effect of Fishing on Clupeoid Production

For many years there have been two schools of thought on the effect of fishing on clupeoid year class survival and its ultimate effect on the fishery. In their joint paper, Clark and Marr (1955) held diametrically opposing views on the merits of density dependency versus independency, but there were a few points upon which they did agree. First, they believed that there must be some minimum spawning stock size below which year class size is a function of stock size, and second, that the magnitude of additions to a population is not determined by the number of eggs spawned but rather the degree of mortality between the time of spawning and when the juveniles or adult fish enter the fishery.

The history of clupeoid fisheries is long enough now to suggest that man has fished near the critical minimum stock size many times. A clupeoid collapse can be due to heavy fishing mortality, which reduces the mean age of the population and forces the very young fish to sustain the reproductive load of the population. If the environment intervenes in some way to cause excessive mortality of the eggs, larvae, or even small juveniles, then at the most, only two successively poor year classes with continued fishing on the adult stock will reduce the population below the critical minimum stock size. This appears to have happened to the Pacific sardine population in 1949 and 1950 (Murphy 1974) and to the Peruvian anchoveta (Fig. 1b). Thus, part of the solution to the "stock–recruitment problem" is to determine for a species the population level below which it will no longer sustain a future fishery should there be some subsequent poor year classes. More important is the need to discover what environmental conditions cause a year class to succeed or fail.

It might also be argued that there is no definable minimum stock size as judged from the observation that clupeoid recoveries are common, albeit unpredictable. An excellent example is the resurgence of the Japanese sardine, *Sardinops melanosticta*, a small, unfishable population (Kondo 1980). In 1972 this residual population gave rise to a formidable year class which has led 11 yr later, to a 3 million t fishery. This is double the tonnage taken at the previous peak of the fishery in 1936 (Fig. 2). Similar year class successes arising from small to virtually nonexistent populations occur from time to time and are not limited to clupeoids, although some other clupeoid species provide similarly spectacular examples, e.g. the Peruvian–Chilean sardine, *S. sagax*. Therefore, barring the unlikely event of the complete extinction of any clupeoid species, there may always be enough fertilized eggs produced, no matter how small the population, to produce a good year class if conditions are right. Just what the "right conditions" may have to be will be examined below.

Hjort's Hypothesis

Johann Hjort, the famous Norwegian fishery biologist, is remembered best for the idea of the "critical period," which he proposed in his 1913 review of the Norwegian herring and cod fisheries (Hjort 1913). He believed that year classes were most probably established in the early post yolk-sac stage of fish larvae when feeding was just beginning (see May 1974 for a discussion of the critical period concept). Hjort felt that spring-spawned herring larvae could not find enough food at the early post yolk-sac stage, and for the most part the larvae were

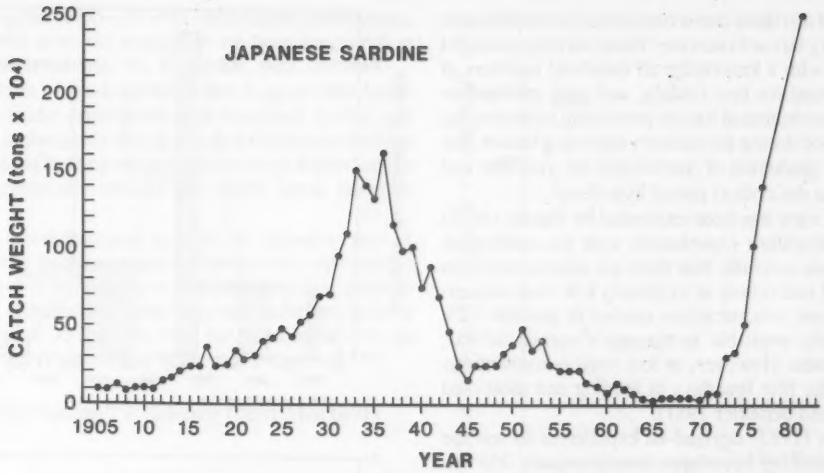

FIG. 2 Catch of the Japanese sardine *Sardinops melanosticta* (after Kondo 1980; Tanaka 1983).

doomed to starve. He reiterated this idea in a provocative paper in 1926 (Hjort 1926). In the latter the suggestion also was made that larval drift could be a mechanism for carrying eggs and larvae out of good food areas.

It has been only in the last three decades that fishery biologists have amassed enough information to begin to tell us whether Hjort was on the right track or not (see review by Blaxter and Hunter 1982). Despite the accumulation of data on the feeding behavior and physiology of the larval herring, sardine, and anchovy, the ultimate experiment, a test of the "critical period" hypothesis, is yet to be done for the herring or any clupeoid. The reason for this is clear: very large data sets on egg production, larval mortality, the larva's environment, and the resulting juvenile survivors are needed over long time periods (probably decades) to obtain the statistical reliability needed with which to test the Hjort critical period hypothesis. However, enough information has accrued in recent years to provide us with the protocol for these studies, and fishery scientists are now in the best position they have ever been to carry them out.

In recent years a number of other ideas have been published on possible year class determinants including interspecific interaction (Lasker and MacCall 1983), cannibalism (MacCall 1980), elaborations of the larval drift idea (Parrish et al. 1981; Nelson et al. 1977), variation in egg survival (Lo 1984), changes in fish fecundity (Picquelle and Hewitt 1983), and the effect of localized oceanographic events (Lasker 1975, 1978) such as stormy periods and upwellings or widespread events such as the unusual warming of the ocean (El Niño) (Valdivia 1978). Some of these depend on the concept of the critical period, i.e. starvation of first-feeding larvae, as the ultimate determinant of the year class, while others emphasize the role of larval survival in density-dependent population regulation.

Food and Feeding of the Clupeoid Larva

There are some generalizations by which the clupeoid larva can be characterized. As hatching it is weak, blind, and depends on endowed yolk to survive. There is evidence that mortality of yolk sac larvae is very great (Picquelle and Hewitt 1983), presumably from predation. At first feeding, a day or so after yolk sac absorption, the larva instinctively snaps at and tries to capture bite-size food particles. However, if it is unsuccessful it will give up trying (Blaxter and Hempel 1963), i.e. there is a "point of no return" behaviorally, and physiologically in a few days if no food (or too little food) is obtained (Blaxter and Hempel 1963; Blaxter and Ehrlich 1974; Lasker et al. 1970; O'Connell and Raymond 1970). What then must the ocean provide to insure larval survival and a good year class? Obviously, nutritious food of the right size must be present in sufficient quantity during the initial feeding of a larva. This is a necessary condition for the larva to pass its first hurdle. Subsequently, predation and transport may increase in importance, but first-feeding larvae clearly face the immediate danger of starvation.

If we accept this premise, recognizing that the quantitative and qualitative details may differ from species to species, a discussion of recent experiments is useful to see if it is possible to derive some predictive principles of recruitment from our knowledge of what a clupeoid larva needs to eat to survive.

The Stability Hypothesis

In a study of anchovy larvae off California (Lasker 1975, 1978, 1981a) I tried to apply laboratory- and field-derived information to the prediction of the relative strength of an anchovy year class. My approach was to determine the threshold number of food particles needed for successful first feeding (Lasker 1975), and then to sample the ocean to find where food concentrations were at, or higher than, the concentrations needed. Off southern California the waters along the coast were usually rich enough to feed anchovy larvae, particularly where there were strong chlorophyll maximum layers. This changed depending on oceanographic conditions, sometimes resulting in the expansion of the geographical area suitable for larval feeding, but at other times limiting successful feeding to the water immediately adjacent to the coast. Occasionally, within the anchovy's spawning season a variety of conditions prevailed such that only a portion of the season could insure a supply of food particles for first-feeding larvae to insure their survival (Lasker 1981a). In another paper (Lasker 1981b) I pointed out that a stable environment is usually needed to allow aggregations of food organisms to form and be

maintained, and that it is these dense concentrations that must be exploited by anchovy larvae to survive. These investigations led me to suggest that with a knowledge of threshold numbers of food organisms needed for first feeding, and with information on what effect the environment has on preserving or destroying concentrations of food during the anchovy spawning season, the basic principles for prediction of recruitment are available and could be used to test the critical period hypothesis.

Another point of view has been expressed by Houde (1978) who observed in laboratory experiments with the subtropical bay anchovy, *Anchoa mitchilli*, that there are always survivors and some growth of individuals at extremely low food concentrations, and that food concentrations needed to produce 10% survival are generally available in the fish's normal habitat, Biscayne Bay, Florida. However, at low food concentrations larvae lost weight the first few days of feeding and most died soon after (Houde and Schekter 1981).

Recently, Methot (1983) devised an experiment to test the critical period and stability hypothesis simultaneously. He was able to determine very precisely the birthdates of juvenile anchovies by counting the number of daily rings on their otoliths (Brothers et al. 1976; Methot and Kramer 1979) and estimated seasonal changes in larval survival by comparing the monthly age composition of juveniles with earlier larval production and the changes in the physical environment encountered by the larvae. This was analyzed for the 1978 and 1979 year classes. Because the northern anchovy has a protracted spawning season (December through May), changes in the environment over the time of spawning should be reflected in the birthdates of the surviving juveniles. Methot found that survival of larvae from December 1977 to March 1978 was less than survival of larvae from April to May 1978, yet larval production was greater in the first part of the season (Fig. 3a). In 1979 this was reversed with survival coinciding with the heaviest larval production in the latter part of the season (Fig. 3b). Because of the violent storms that occurred in the winter of 1977–78, I predicted that there should be poor survival in the first half of the spawning season for that year with comparatively better survival as a reflection of calm conditions which prevailed from mid-March 1978 to the end of the spawning season in May.

The violent ocean conditions caused by the early 1978 storms kept the ocean sufficiently mixed and too dilute with respect to larval fish food organisms until March when aggregations of potential food organisms appeared (Lasker 1981b). Methot (1983) pointed out, however, that recruitment of the 1979 year class was poorer than in 1978, especially during the latter portion of the spawning season. This pattern seems better explained to him by indices of offshore transport than by indices of food availability for larvae, but the seasonal pattern of survival in 1978 could not be explained by transport. He suggested that both conditions may account for the differences found.

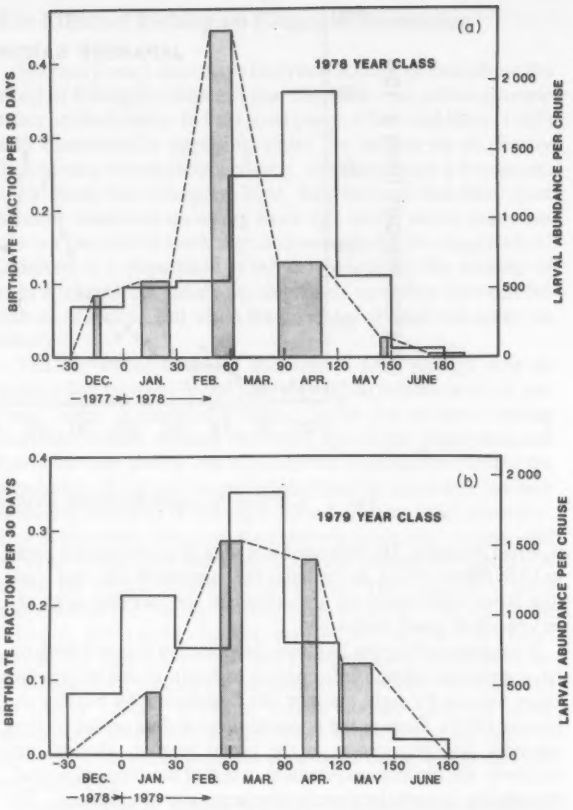

FIG. 3. Comparison of the seasonal distribution of birthdates of juvenile anchovy (open histogram) to the seasonal distribution of larval abundance (stippled bars; the width of these bars indicates individual survey duration). Note that survivorship did not coincide with major larval production in 1978 (a) but did so in 1979 (b). However, total survivorship was better in 1978 than 1979, causing a twofold greater recruitment in the earlier year relative to the latter (after Methot 1983).

Mechanisms of Larval Transport

Parrish et al. (1981) investigated the reproductive strategies of the most successful fish stocks off California and how these relate to a variety of oceanographic conditions. They concluded that successful fish in the California coastal region minimize their offshore loss of reproductive products by choosing to spawn in areas and at times when upwelling and offshore transport are at a minimum. Thus, they hypothesized that deviations from "normal" transport conditions could have profound detrimental effects on a year class by carrying eggs and larvae to areas where there is not enough food to survive. A variant of this idea is the report by Shelton and Hutchings (1982) that the eggs and larvae of the South African anchovy, *Engraulis capensis*, are carried from an area of poor productivity to one of high productivity by a surface frontal jet. When transport slackens, high mortality is the rule.

One of the more interesting studies of larval transport was published by Nelson et al. (1977). They presented convincing evidence that good year classes of menhaden, *Brevoortia tyrannus*, depend on environmental conditions that favor the drift of eggs into estuaries of the east coast of the United States where the larvae presumably find good feeding conditions. They produced a multiple regression model relating recruitment to the following environmental variables: (1) Ekman transport rates from three areas where menhaden abound, (2) the minimum mean sea surface temperature at the mouth of Delaware Bay in the year class year, and (3) the sum of monthly average discharge rates from three rivers in July–September of the year preceding the year class year. These authors used a data

set covering the years 1955–70 with remarkable correlations. However, in recent years the model has not been successful in predicting year class success (W. E. Schaaf, pers. comm.).

Another variation of the hypothesis that suggests that larval transport may regulate populations was described by Iles and Sinclair (1982). In this study they presented the interesting idea that the magnitude of herring subpopulations may depend on the size of oceanographically isolated but stable larval retention areas.

In summary, larval transport may be an effective way of sweeping relatively helpless clupeoid larvae into unfavorable areas or conversely of moving them to areas where they can find optimal survival conditions. Either way the basis for survival is the coincidence of larvae with food for them to survive, as suggested in the Hjort hypothesis of the critical period.

Predation or Starvation? Evidence from Mortality Curves

The literature on clupeoids has blossomed with information on their predators and in some cases how much is eaten. The review by Blaxter and Hunter (1982) provides an excellent summary on predation of eggs and larvae by invertebrates and fishes, including a discussion of the incidence of cannibalism. Undoubtedly, predation at all stages of the life of any planktonic organism must rank high among those factors that regulate its population size. The difficulty has been and continues to be the quantification of predation. Population dynamicists have usually resorted to indirect measures considering the fraction of mortality not accounted for by other means as being due to predation. Hunter (1982) in a recent review article concluded from a series of mortality curves obtained for the northern anchovy that the smooth monotonic exponential decrease in numbers of eggs and larvae "lays to rest the Hjort hypothesis of a high larval mortality resulting from starvation beginning at yolk absorption" at least for the Northern anchovy. His thesis is that egg and larval mortality is most probably a density-dependent result of predation, particularly if the predators are invertebrates that appear in blooms (e.g. the jellyfish *Aurelia*, Möller 1982), or due to filter-feeding fishes, as anchovy adults eating their own eggs and larvae (cannibalism, Hunter and Kimbrell 1980). However, mortality rates are too imprecise to afford us a definite conclusion on this point, and I believe it is premature to discard the "critical period" idea. The mortality curve shown in Fig. 4 is typical of those obtained for the northern anchovy. It is derived from the number of eggs and larvae obtained over a 40-d period in the midst of the anchovy spawning season and from an area over thousands of square kilometres. Corrections are made for a variety of factors, such as extrusion of a proportion of the eggs and larvae through the meshes of the plankton net used to collect them, avoidance of the collecting net as the larvae grow older, adjustment for the individual larval growth rates, and the application of two models, one age-independent instantaneous mortality rate for eggs and an age-dependent mortality rate for larvae (Lo 1984). Since the most precise mortality curves show no apparent critical period, it either does not exist as a distinct portion of the mortality curve or it is essentially not provable by current field methods. Blooms of predators, such as jellyfish in Kiel Bight (Möller 1982), should in themselves provide a break in the mortality curve that we would normally ascribe to a critical period, particularly if predators are size-selective in their feeding and the spawning season is a protracted one. However, none has been detected thus far.

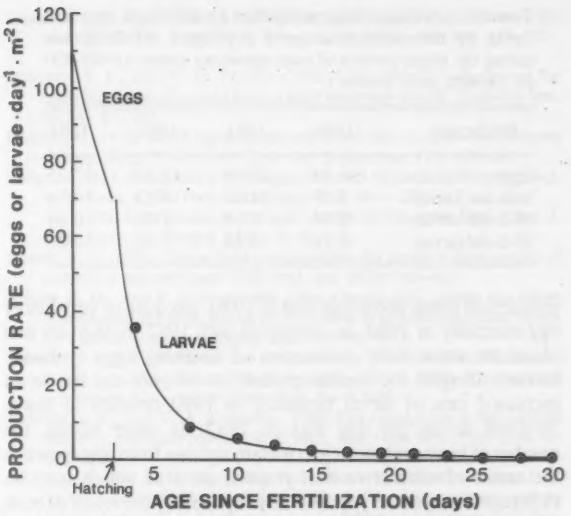

FIG. 4. Mortality curve for eggs and larvae of *Engraulis mordax*, 1983 (after Picquelle and Hewitt 1983). See text for explanation.

Oceanographic Events

It is impossible to consider the fate of pelagic fish without an examination of the effect of the environment on mortality. Parrish et al. (1983) examined a number of environmental processes in relation to anchovy and sardine reproduction in Eastern Boundary currents. They concluded that, in general, upwelling centres seem to be avoided by spawning clupeoids. Yet they also pointed out that the large Peruvian anchoveta population is an exception, since it spawns in an area of strong upwelling. However, upwelling is much stronger off Peru in the summer when spawning is weak as compared with the winter spawning season. In other words the anchoveta lives in an upwelling area known to be extremely rich in forage but minimizes the detrimental effects of upwelling, e.g. offshore transport, by choosing the least oceanographically energetic time to deposit its eggs. These authors showed that spawning tends not to occur in regions where wind conditions would cause turbulent mixing of the upper water column, and this is characteristic of the Peruvian upwelling area. The conclusion from their study is that there has been a strong natural selection acting on clupeoid populations to produce a massive number of eggs over a long spawning season during times and in latitudes where the eggs and larvae are at least risk.

Variable Egg Production and Differential Mortality

Since 1980, scientists at the Southwest Fisheries Center have been perfecting a technique for biomass assessment of the northern anchovy, the egg production method first described by Parker (1980) and now used routinely on an annual basis (Picquelle and Hewitt 1983). Table 1, derived from four years of egg and larva sampling in the California Current, encompassing the entire spawning range of the central population of the northern anchovy, shows the results of differential spawning and mortality of eggs and larvae from year to year. For example, a comparison between 1980 and 1982 shows markedly different egg production between the two years, with 1982 total egg

TABLE 1. Average daily production ($\times 10^{12}$/d) of eggs and larvae by the northern anchovy population off California during the major portion of each spawning season (1980–83) (R. Hewitt, pers. comm.).

Production	1980	1981	1982	1983
Eggs	26.34	20.96	13.51	17.25
Yolk-sac larvae	7.18	14.34	8.53	10.78
10-d-old larvae	0.74	1.59	1.04	0.69
30-d-old larvae	0.10	0.24	0.16	0.07

production being about half that of 1980. Because of very heavy egg mortality in 1980, as compared with 1982, both years had about the same daily production of hatching eggs (yolk-sac larvae). Despite the similar production of yolk-sac larvae an increased rate of larval mortality in 1980 resulted in fewer 30-d-old larvae per day than in 1982. In other words, the number of larvae remaining to metamorphose from any spawn is the result of several mortality rates, each of which may be different from year to year and all are probably the result of both biotic (predation) and abiotic (oceanographic) factors. This is dramatically illustrated in Fig. 5, which shows to what degree the average daily egg production over the entire area of northern anchovy spawning can change from year to year. Lo's (1984) analysis of 30 yr of anchovy egg production off the west coast of the United States and Mexico shows that there have been occasional bumper crops of anchovy eggs but not necessarily concomitant good year classes. For example, 1975 was an enormously successful year for egg producton (Fig. 5) and primary production (Smith and Eppley 1982), but the end result was a disastrous year class (Lasker 1981a), the worst of 16 consecutive year classes analyzed. Lasker (1981a) believes that the root cause of this poor year class could be attributed to the presence of a dominant but nutritionally poor larval food source, the dinoflagellate *Gonyaulax polyedra*, which was above the threshold-for-feeding concentrations during the first half of the spawning season, and to the untimely onset of strong upwelling thereafter, which resulted in high production of inedible diatoms.

El Niño Events

The waters off Ecuador, Peru, and Chile historically have had exceptionally large clupeoid fisheries. Upwelling of nutrient-rich water has been the trophic underpinning of these fisheries by supporting an extremely rich phytoplankton fauna fed upon directly by filter-feeding anchoveta and sardines. From time to time, invasions of unusually warm nutrient-depleted water occur, an El Niño, which have, on some occasions, coincided with the collapse of the coastal clupeoid stocks off these nations (Fig. 1a). As Valdivia (1978) pointed out, there is a behavioral modification of anchovy movement and subsequent distribution during an El Niño. Off Peru, the anchoveta drastically reduced the area it occupied during the 1972 El Niño, so that in March, April, and May 1972, large concentrations of fish schooled close to the coast and became unusually available to the coastal fishery. Anomalous spawning of the anchoveta also occurred from September 1971 through May 1972, with a markedly reduced production of eggs. The combination of extremely heavy fishing, which undoubtedly pushed the anchoveta population below its minimum stock size, and the obvious failure of one or more of the following year classes caused the collapse of

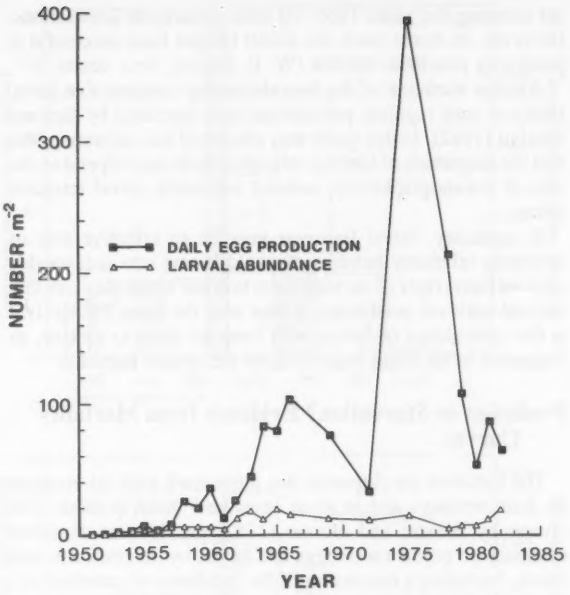

FIG. 5. Daily egg and larval production of *Engraulis mordax* in the California Current over a 30-yr period. The year 1975 was characterized by an enormous spawning but poor larval survival (after Lo 1984).

the fishery with its attendant disastrous economic consequences (Murphy 1974).

While there has been a gradual but persistent return of the sardine to Peruvian and Chilean waters in recent years, there have also been several El Niño events. The severe El Niño of 1983, which began in September–October 1982, was characterized by disruption of anchoveta and sardine schools. In some instances, sardines accumulated "in some small areas" according to Jordan (1983), which made it appear that sardines were abundant, but these were rapidly fished out.

Whether El Niño events affect the survival of fish eggs and larvae is currently undocumented and remains to be investigated. In California the El Niño of 1983 was manifested by a much wider distribution of spawning anchovies than occurred in previous years contrary to the contraction found in Peru. Per capita egg production seemed to be relatively unaffected in California. The amount and extent of surface warming with which the fish had to contend was much different between Peru and California, the habitat in Peru always exhibiting a greater temperature differential and more drastic effects on the behavior of the fish (Fig. 1a).

Competition

Do coexisting species of pelagic fish that inhabit thousands of square miles of ocean compete for food resources and space? This intriguing question has never been answered satisfactorily. Lasker and MacCall (1983) investigated this question indirectly by inferring the relative mean sardine and anchovy size from frequency distributions of sardine and anchovy scales found in anaerobic sediments. The average anchovy size from periods of high sardine abundance was found to be significantly smaller than in periods when sardine populations were low. The authors pointed out that this result is consistent with a competition hypothesis but that there are other possible explanations, e.g.

offshore distribution of small anchovies. An occasional response of an ecosystem when sardines are low in abundance (e.g. off California) is an increase in the population of anchovies, and alternatively, some ecosystems where anchovies are reduced (e.g. Peru–Chile), sardines have increased in number remarkably. Whether competition on a large geographic scale is the causal mechanism has yet to be decided.

Conclusion

The answer to the question, "what limits clupeoids?," seems to be "almost everything." More realistically, the question should be phrased "what limits clupeoids mostly?" Other questions follow this one: When, in the life cycle, does this occur? What are the interrelationships between limiting factors and between species? What can be learned from species life histories and fishery oceanography that will allow us to predict recruitment?

A review of the literature shows that we are on the threshold of significant investigations that may provide the answers to these questions. Studies, such as those conducted by Methot (1983), seem to be the most promising for isolating the factors affecting the recruitment of a year class. The Methot experiment allows us to look back at the environment to see which factors were present or absent when there was good or poor survival within a spawning season when a year class was produced. With a time series of such studies on the same species it seems likely that the factors that are responsible for formation of a year class can eventually be identified.

In the international sphere this approach has been suggested for IREP, the International Recruitment Program, by Working Group 67 of SCOR (Scientific Committee on Ocean Research), intending that several nations work simultaneously on the same fish species group so that data bases could be amassed and compared throughout the world. The essential data can be collected through the use of the newest technological tools available in fisheries research, which include determination of birthdates, growth rates, and ages of fish larvae and recruits using counts of daily rings of the otoliths, the egg producton method to obtain total population fecundity, sampling of the biotic environment by sophisticated nets, pumps, and high frequency sonar, and the monitoring of oceanic parameters with the variety of ocean measuring devices perfected by physical oceanographers in recent years.

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Session 2: Spawning, Development, and Survival of Early Life Stages of Herring

Distribution and Characteristics of Herring Spawning Grounds and Description of Spawning Behavior[1]

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Pacific herring (*Clupea harengus pallasi*) are winter–spring spawners which exhibit a south to north latitudinal cline in spawning time. In the eastern Pacific, major spawning populations are concentrated near San Francisco, in Puget Sound, and along the coasts of British Columbia and southeastern Alaska. In the Bering Sea, herring spawn in Alaska and along the Kamchatka Peninsula. In the western Pacific, herring spawn in the Sea of Okhotsk and the Japan Sea. Atlantic herring (*Clupea harengus harengus*) consist of both winter–spring and summer–autumn spawning groups characterized in the northeast Atlantic by oceanic, shelf, and coastal populations. The oceanic group are large migratory fish spawning off the coasts of Norway and Iceland. The shelf group includes the various locally migratory North Sea populations adjacent to the British Isles. The coastal groups consist of smaller fish restricted to the Baltic and White seas. In the northwest Atlantic, spawning occurs from northern Labrador to Virginia with spring spawners predominating in the north and fall spawners in the south. Herring typically congregate near their spawning grounds for several weeks to months prior to spawning. Temperature is one of the factors that determine when spawning occurs. The Atlantic herring exhibits sexual dimorphism in the spawning act with only the female interacting with the spawning substrate. Both sexes of the Pacific herring make physical contact with the substrate on which the adhesive eggs are deposited. Spawning grounds are located in high-energy environments, either nearshore for spring spawners or in tidally active areas for fall spawners. Spawn is deposited on marine vegetation or on bottom substrate, such as gravel, which is free from silting. The eggs are tolerant to temperatures in the range of 5–14°C and salinities in the range of 3–33‰. Egg mortality results mostly from suffocation due to high egg densities and silting, predation, and, in intertidal spawn, from stresses imposed by exposure to air and from egg loss by wave action.

Le hareng du Pacifique (*Clupea harengus pallasi*), qui fraye en hiver et au printemps, exhibe un cline latitudinal du sud au nord au moment de la fraie. Dans le Pacifique oriental, les principales populations reproductrices sont concentrées près de San Francisco, dans le Puget Sound et le long des côtes de la Colombie-Britannique et du sud-est de l'Alaska. Dans la mer de Béring, le hareng fraye en Alaska et le long de la péninsule de Kamchatka tandis que, dans le Pacifique oriental, il se reproduit dans la mer d'Okhotsk et la mer du Japon. Les harengs de l'Atlantique (*Clupea harengus harengus*) se composent de groups qui frayent pendant la période hiver–printemps et été–automne, groupes caractérisés dans l'Atlantique nord-est par des populations peuplant l'océan, la plate-forme ou les côtes. Le groupe océanique est composé de gros poissons migrateurs qui se reproduisent au large de la Norvège et de l'Islande, tandis que celui de la plate-forme compte les diverses populations qui migrent localement dans la mer du Nord près des îles Britanniques. Par contre, le groupe côtier consiste en de plus petits poissons restreints aux mers Baltique et Blanche. Dans l'Atlantique nord-ouest, la fraie a lieu du Labrador septentrional à la Virginie; les reproducteurs printaniers se concentrent au nord et les géniteurs d'automne, au sud. Typiquement, le hareng se regroupe près des frayères pendant plusieurs semaines ou mois avant la fraie. La température représente un des facteurs qui déterminent le moment de la fraie. Lors de l'accouplement, le hareng de l'Atlantique exhibe un dimorphisme sexuel : seulement la femelle interagit avec le substrat de la frayère. Par contre, chez le hareng du Pacifique, les deux sexes entrent en contact physique avec le subtrat, où les oeufs adhérents sont déposés. Les frayères sont situées dans des environnements à haut potentiel énergétique, soit près des côtes pour les reproducteurs printaniers ou dans les zones à marée active pour les géniteurs automnaux. Le frai est déposé sur la

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végétation marine ou sur un substrat comme du gravier non exposé à l'envasement. Les oeufs supportent des températures variant de 5 à 14°C et des salinités de l'ordre de 3 à 33‰. La mort des oeufs est due en grande partie à la suffocation causée par de fortes densités d'oeufs ainsi qu'à l'envasement, à la prédation et, dans le cas du frai déposé dans les zones intertidales, aux stress imposés par l'exposition à l'air et à la perte par l'action des vagues.

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The herring of the temperate Northern Hemisphere are known to inhabit the Pacific, Atlantic, and Arctic oceans. They are presently considered to represent two subspecies: the Atlantic herring *Clupea harengus harengus* and the Pacific herring *Clupea harengus pallasi* (Bailey et al. 1970). Both species exhibit a remarkable plasticity in the time, place, and environmental conditions in which reproduction occurs. Consequently, there is some uncertainty about the degree of overlap in the distribution of the two subspecies along the Canadian and Russian Arctic shorelines.

The characterization of distinct populations within these two subspecies on the basis of morphology, meristics, growth, maturation, and spawning time preoccupied the early researchers in all areas (Tester 1937; Heincke 1898; Johansen 1924). However, Blaxter (1958) emphasized that although differences in these characters may suggest genetic differentiation, for populations to be genetically distinct units from a taxonomic and management viewpoint reproductive isolation was imperative. Clearly the variability in spawning times and places suggested the existence of genetically distinct "subraces," but in general insufficient biological information was available to conclusively demonstrate this. Only recently has there been a general concensus that herring "home" to their spawning grounds with consistent fidelity (Zijlstra 1958, 1963; Hourston 1982), and thereby effect the reproductive isolation that could manifest itself in genetic differentiation within the two subspecies.

The characterization of the locations in which, and conditions under which, herring are able to reproduce themselves is therefore crucial to our understanding of the taxonomic status of these species and thereby their effective conservation and management. Hence, this paper attempts to collate the available literature on recognized herring stocks, the characteristics of the associated spawning grounds, and what is known regarding factors that initiate and affect spawning behavior.

Pacific Herring (*Clupea harengus pallasi*)

Distribution of Stocks and Spawning Grounds

Pacific herring are virtually all winter–spring spawners although there are some isolated instances of unusually early and late spawning populations. Spawning occurs in the intertidal and upper subtidal zones and is characterized by the milky white appearance of the water. Pacific herring inhabit waters of the continental shelf and spawn along the shoreline from southern California to Korea (Fig. 1 and 2).

East shore Pacific Ocean

In California, herring spawn in estuarine and bay regions from San Diego to Humboldt bays (Miller and Schmidtke 1956), with most of the egg deposition occurring in Tomales and San Francisco bays. In Oregon, spawning has been reported from seven estuaries (Butler 1980). Along the coast of Washington State there have been reports of spawn in Grays Harbor and Willapa Bay, and herring spawn regularly in Puget Sound and from the entrance of Puget Sound to the Canadian border (Penttila and Day 1976).

Herring spawn is found throughout the coast of British Columbia, including the east and west coasts of Vancouver Island, the many smaller islands in Georgia and Johnstone straits, along the mainland coast from the Washington to the Alaska borders and on the shores of the many islands along this same coastline, and in the Queen Charlotte Islands (Haegele and Fitzpatrick 1983). In British Columbia, over 3000 km of coastline have been utilized by herring for spawning, and yearly depositions extend along an average of 400 km of coastline.

In southeastern Alaska, herring spawn on the many islands and along the mainland coast with the main spawning areas in the vicinities of Ketchikan, Craig, Frederick Sound, Auke Bay, and Sitka (Skud 1959).

Bering Sea

Along the Alaska shore of the Bering Sea, herring spawn from Atka Island in the Aleutian Chain to Kotzebue Sound with the greatest concentration of spawn in the Togiak District of Bristol Bay (Barton and Wespestad 1980). In the western Bering Sea, herring spawn at the southwest entrance to Korfu Bay in years of low stock abundance. In years of high abundance they spawn from Korfu Bay along the Kamchatka Peninsula to a point opposite Karaginski Island, on the southwest shore of which they also spawn (Iizuka et al. 1969). The amount of spawn deposited by Korfu–Karaginski herring has been recorded to have ranged between 1.3 and 16.0 km^2 (Morita 1982).

Sea of Okhotsk

The herring of the Okhotsk Sea spawn in Shelekov Bay along the inside of the Kamchatka Peninsula and in Ghizhiginsk Bay and from Tauisk Bay to Ayan (Ayushin 1963).

Japan Sea

In the Japan Sea there appear to be several populations of herring whose relative abundances have changed over the past century causing some changes in spawning locations (Irie 1980). The northernmost population are herring that spawn in DeKastri Bay. The Sakhilin herring spawn on the southeast and southwest shore of Sakhilin and in Aniva Bay. The Hokkaido "spring" herring spawn along the west and northeast coasts of Hokkaido, the southern limit being Ishikari Bay. There is also a smaller population that spawns on the Pacific coast of Hokkaido (coast of Abashiri) and several lake-spawning stocks: Notorro and Akkeshi on Hokkaido and Obuchi and Hinuma on Honshu (Motoda and Hirano 1963). Herring also frequent the waters near and are reported to have spawned on the shores of Korea.

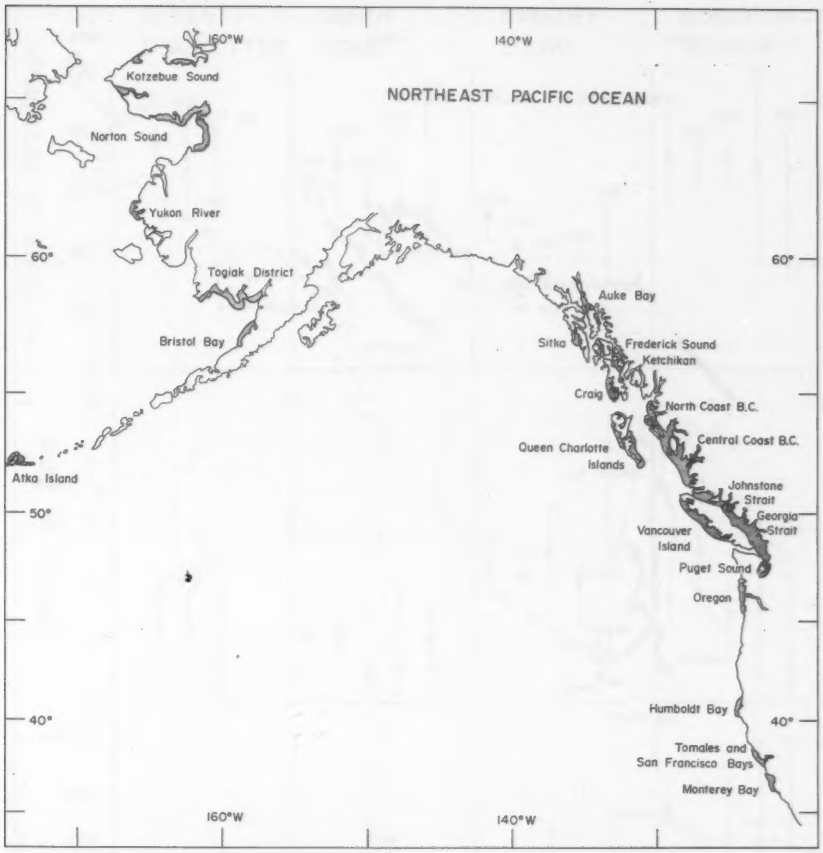

FIG. 1. Herring spawning stocks and grounds of the northeast Pacific.

Spawning Ground Characteristics

Time of spawning

Pacific herring exhibit a south to north cline in spawning times (Fig. 3). Spawning may begin in November in California and may be as late as July in Kotzebue Sound in Northern Alaska. The time of spawning may vary from year to year within any major geographical area; however, peak spawning generally occurs within a 3- to 6-wk period, although spawning may extend over 2 mo. Initial and concluding spawns are generally quite small, while spawns in the peak period are extensive. Within the peak period, there are frequently two major waves separated by a 2- to 4-wk period. In British Columbia the spawns of the first wave are usually greater and involve about three quarters of the spawning population of an area. The very early and very late spawns within an area are usually deposited by what are thought to be nonmigratory resident stocks. In the Queen Charlotte Islands, spawns are always early (early March) in Naden Harbor and always late (mid-May) in Skidegate Inlet, while the majority of the spawns, which are deposited in the other sounds and inlets of the islands, occurs in April (Hourston 1980). In Lake Notorro on Hokkaido the landlocked form always spawns earlier than the migratory form (April–May vs. May–June) (Kanno 1981). In central British Columbia the stocks spawning in Burke Channel always do so in late May and early June, while on the outer coast at the entrance to this channel spawning occurs from mid-March to mid-April. The early and late spawning stocks cited as examples can all be separated from the major migratory stocks on the basis of age composition of the schools and growth rates.

Location of spawning grounds

Throughout their range Pacific herring spawn along shorelines and under conditions of remarkable similarity. Almost exclusively spawning does not occur on the open coastline but is restricted to inlets, sounds, bays, and estuaries that are somewhat sheltered from the surf of the ocean. In California and Oregon, spawning occurs only in bay and estuarine regions; in Washington State there has been no spawn found in the only partially protected waters of Juan de Fuca Strait from Port Angeles to Grays Harbor; on the south and southwest coast of Vancouver Island there is no spawn between Victoria and Barkley Sound except in the sheltered waters of Sooke Basin, Port Renfrew, and Nitinat Lake. This situation recurs on the west coast of the Queen Charlotte Islands, in the Bering Sea, and in the western Pacific Ocean. The selection of sheltered shorelines for spawning is probably an adaptation to minimize egg loss. The wave action resulting from storms can uproot the vegetation on which the eggs are laid and cast the eggs ashore. Even in relatively sheltered waters this egg loss can be substantial (Hay and Miller 1982).

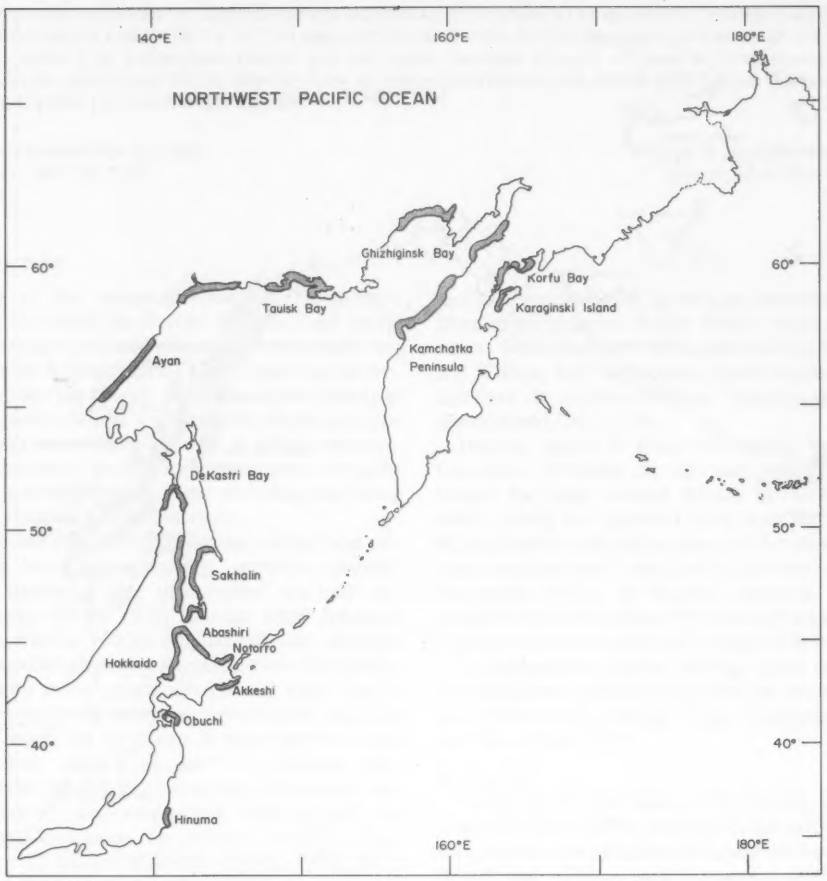

FIG. 2. Herring spawning stocks and grounds of the northwest Pacific.

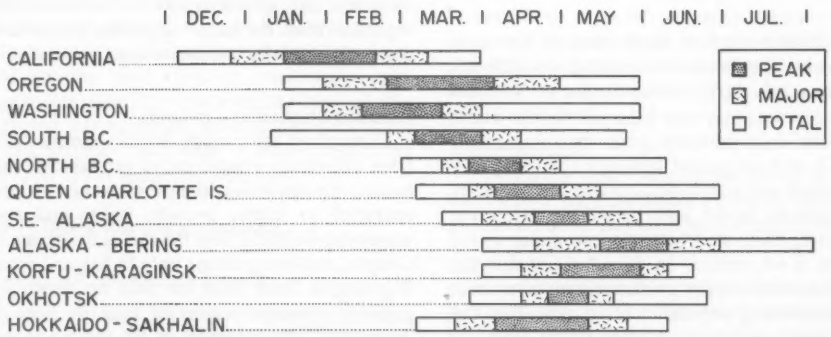

FIG. 3. Timing of Pacific herring spawnings by major stock groupings.

Egg distribution

Eggs are laid almost exclusively on marine vegetation, algae and sea grasses, although quite frequently eggs adhere to the rocky substrate to which the algae are attached. Egg density can vary from a few thinly scattered eggs to more than 20 layers, and for individual spawns the average number of eggs may vary from $1.00 \times 10^5/m^2$ for light-density spawns to $1.00 \times 10^6/m^2$ for moderately high-density spawns (J. F. Schweigert, C. W. Haegele, and M. Stocker, submitted). At heavy egg densities of five layers on dense vegetation about 3.00×10^6 eggs/m^2 are deposited (Schweigert and Fournier 1982). At an average fecundity of 3.0×10^4 eggs, between 3 and 100 female herring would utilize 1 m^2 of spawning ground.

Although eggs may be deposited to depths of 20 m, the

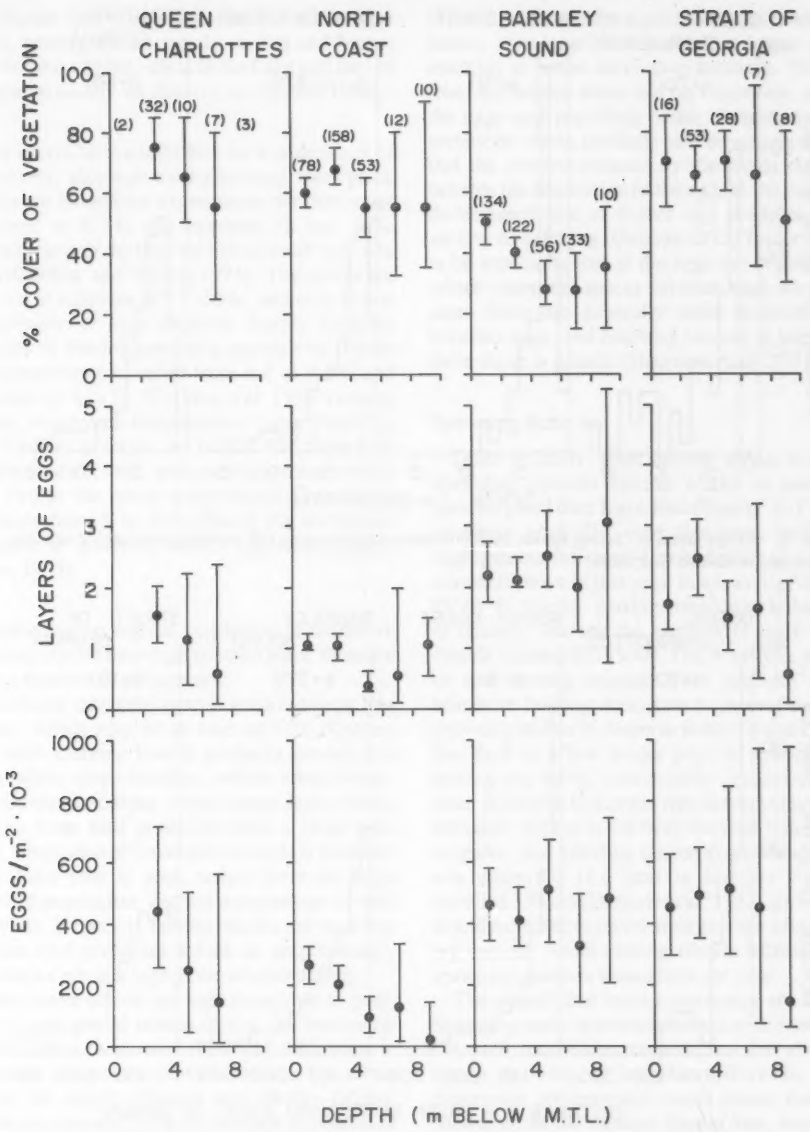

FIG. 4. Percent cover of vegetation, layers of eggs, and eggs per square metre (Wilcoxon median and 95% C.I.) by depth (metres below mean tide level at spawning) for spawns at selected locations in British Columbia.

heaviest egg deposition occurs where the vegetation is the densest, which is in the lower intertidal and upper subtidal zone (Fig. 4). In British Columbia, where spawns have been sampled and surveyed by SCUBA divers at a number of locations (e.g. Haegele and Schweigert 1985; Haegele et al. 1981), most of the spawn has been deposited within 10 m of the mean tide level at spawning (Fig. 5). Spawns may be in excess of 400 m wide, but 90% of spawn occurred within 150 m of the inshore edge of the spawning (Fig. 6).

The density of egg deposition and the width of spawn may be stock size dependent. There have been several documented cases that the spawn produced by small stocks is generally lighter and narrower than the spawn produced by larger stocks. In California, spawn density was generally two to three layers in San Francisco Bay when stocks were estimated at 12 000 t, while in Tomales Bay spawn produced by a stock of 4000 t was generally less than one layer (Miller and Schmidtke 1956), and spawns in Humboldt Bay, where stocks were estimated at 300 t, were less than one-quarter layer (Rabin and Barnhardt 1977). In Washington State, spawns in Puget Sound, where the population was estimated at 5000 t, were very light, while in the United States portion of the Strait of Georgia, where the population was estimated at 15 000 t, the spawns were of medium density (Trumble et al. 1977). In British Columbia the spawns of a stock at a low level of abundance (north coast) had significantly lower egg densities (Fig. 4) and the spawn was

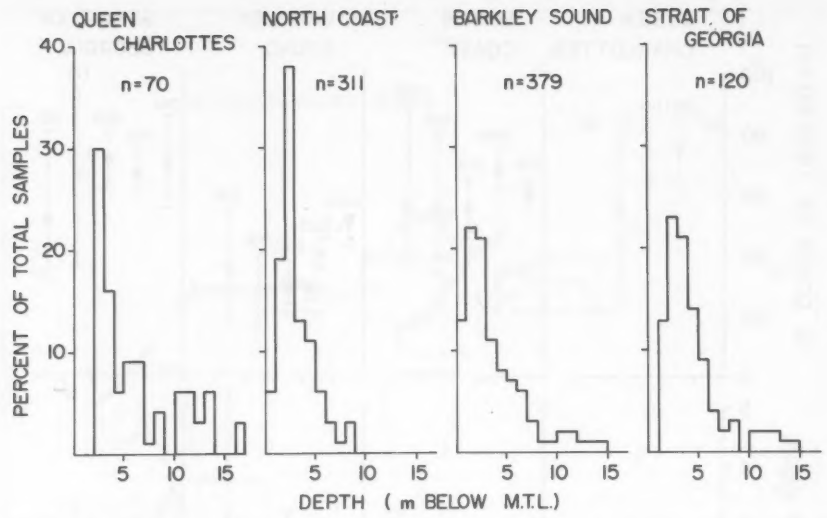

FIG. 5. Distribution of herring spawn by depth (metres below mean tide level at spawning) at selected locations in British Columbia.

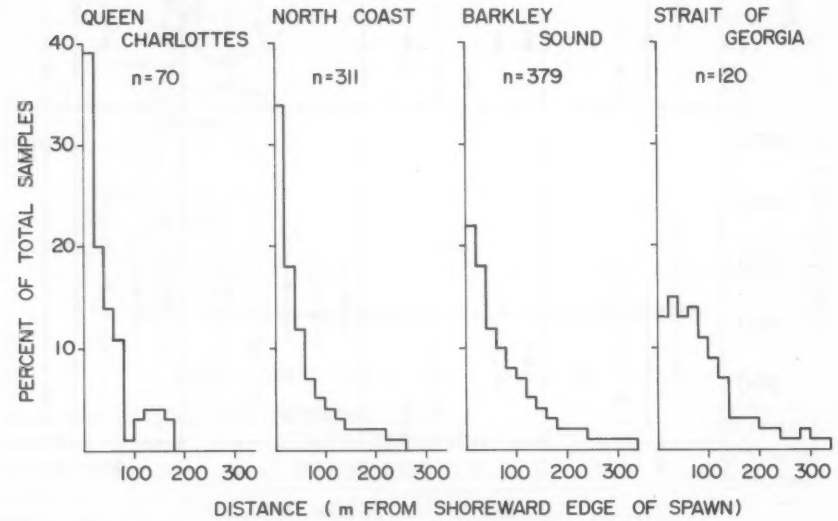

FIG. 6. Distribution of herring spawn by width at selected locations in British Columbia.

significantly narrower (Fig. 6) than for stocks at medium levels of abundance (Strait of Georgia, Barkley Sound). Galkina (1971) observed that "spawn in a single layer or thinly scattered occurs in regions where herring are not abundant, e.g., in the southeast Barents Sea, in some parts of the White Sea, and also in other seas at periods with comparatively poor stocks." In Hokkaido, during the early 1950's, it was observed that spawns were gradually becoming narrower (Tamura et al. 1955) at a time when the population was dominated by the 1948 year-class during the collapse of the fishery (Motoda and Hirano 1963).

Herring do not appear to favor one type of vegetation as a spawn substrate over another, and the type of vegetation upon which the eggs are laid is a function of the depth at which the eggs are deposited and the type of vegetation found in a given area. It has been calculated (Haegele et al. 1981) that less than 25% of total spawn becomes exposed to air and then only for a brief period, about 10% of the total incubation time. In British Columbia, exclusive of the Queen Charlotte Islands, 30% of eggs are laid on *Zostera* sp., 10% on *Fucus* sp., 20% on broad-leafed kelp and other brown algae, and 40% on red algae, mostly of the filamentous type. In other parts of their range herring spawn on similar marine vegetation. In California and Puget Sound, *Zostera* sp. and shallow-water filamentous red algae are the dominant spawn substrates (Miller and Schmidtke 1956; Gonyea et al. 1982). In the Queen Charlotte Islands, where the giant kelp, *Macrocystis* sp., occurs nearshore and in sheltered inlets, it is an important spawn substrate (Haegele and Schweigert 1985). In southeastern Alaska, spawn substrates are similar to those of British Columbia (Blankenbeckler 1977), while in Bristol Bay most of the spawn is deposited on *Fucus* sp.

and *Zostera* sp. (Barton and Wespestad 1980). On the west shore of Hokkaido, herring spawn mostly on red and brown algae (Tamura and Okubo 1953b), while in the Lake and Bay of Akkushi, herring spawn mostly on *Zostera* sp. (Iizuka 1966).

Environment

Herring eggs and sperm have a tolerance for a wide range of temperature and salinity, although most spawning takes place over a narrow range. In laboratory experiments the maximum viable hatch occurred at 8.3°C and between 12 and 26‰ salinity, and the lower limit of the thermal tolerance of eggs was found to be 4°C (Alderdice and Velsen 1971). The sperm are able to survive for 4 d at salinities of 17–33‰, and only below 5‰ does the fertilization of eggs decrease sharply (Galkina 1957). In situ studies of herring spawning grounds in British Columbia found temperatures to range from 6.5 to 9.8°C and salinities to range from 22.4 to 28.7‰ (Hay et al. 1984; Outram 1975). In California, incubation temperatures range from 8 to 10°C (Miller and Schmidtke 1956), in Bristol Bay from 6 to 10°C (Barton and Wespestad 1980), with incubation times of 6 d at the higher and 18 d at the lower temperature. Changes in salinity over the range from 6 to 34‰ during the incubation period do not appear to adversely affect egg development (McMynn and Hoar 1953).

Egg survival

Although, by spawning on marine vegetation in nearshore waters, Pacific herring expose their eggs to some risks, these are probably offset by a number of advantages.

Spawn deposited in the intertidal zone is subject to egg loss from bird predation, which may be as high as 40% (Outram 1958). However, such extreme loss is probably confined to large spawns on shallow slope beaches, which attract birds. Small spawns or spawns in deeper water attract few, if any, birds. Loss of eggs from bird predation over a large geographical area (e.g. west coast of Vancouver Island) is probably a constant amount from year to year, unless there are large fluctuations in the bird population, and not a percentage of total spawn (Outram 1958). Hence, if herring stocks are at a low level, egg loss from bird predation would be proportionally higher than when stocks are at a high level of abundance.

Loss of eggs from wave action can vary from year to year, depending on the occurrence of storms during the incubation period. On Rishira Island there was a 14-fold difference in successive years in the amount of spawn torn loose by storms and washed up on the beach (Tamura and Okubo 1953a). Typically, during heavy storms, 25% of the eggs deposited in the immediate vicinity may be washed up on the beach (Hay and Miller 1982) or 40% of eggs in the intertidal zone may be lost to storm action (Outram 1958). Depending on how high on the beach the eggs were cast and at what stage of development the eggs were dislodged, the egg mortality varies. The hatching rate of eggs cast up on shore may be only slightly less than for eggs remaining attached if the eggs are close to hatching when dislodged (Hourston and Rosenthal 1976b), and eggs have been observed to survive for 6 d if the eggs are wetted by wave action (Tamura and Okubo 1953a).

Intertidal exposure also subjects attached eggs to the stresses of dehydration and fluctuations in temperature and salinity. This exposure can increase prehatching mortality of eggs from 10 to 30% (Jones 1972).

There appear to be some not well-understood or documented advantages to depositing eggs on marine vegetation in shallow nearshore waters. The surface area available for egg deposition is much greater on the algae for any given area of ocean bottom; hence, eggs can be deposited at lower densities, probably resulting in better survival to hatching. The eggs are elevated from the bottom when laid on vegetation, preventing silting of the eggs and providing better circulation for the removal of metabolic waste products and oxygenation. It is conceivable that the oxygen released by the plants during photosynthesis benefits the respiration of the eggs in the inner layer. It has been documented that at higher egg densities fewer of the eggs survive to hatching (Galkina 1971; Taylor 1971). This appears to be especially true if the eggs are deposited on flat surfaces where interstitial spaces between eggs are small. On branched algae there are generally more frequent and larger spaces between eggs, and hatching success at higher egg densities on these algae is greater (Hourston et al. 1981).

Spawning Behavior

Quite typically, adult herring appear to congregate near the spawning grounds several weeks to months in advance of spawning and then leave immediately. In California, first-wave spawners gradually enter the bays, building up into large aggregations for several weeks prior to spawning there; later spawners move in just prior to spawning (Miller and Schmidtke 1956). In Alaska, herring congregate in lagoons from October to January, leaving the lagoons in April and May to spawn outside (Rounsefell 1930). The more typical situation appears to be that herring migrate from offshore feeding grounds to nearshore holding areas one to several months in advance of spawning to finally disperse to the ultimate spawning location a few days to a few weeks prior to spawning. Ripe and spent herring can travel considerable distances in a short period of time. In British Columbia ripe herring tagged prior to spawning travelled 150 km in 6 d from Barkley Sound to Esperanza Inlet to spawn, and a herring tagged at spawning in Lambert Channel was recovered 16 d later in Juan de Fuca Canyon, having travelled 350 km (Haegele et al. 1982). In both instances the fish would have had to travel at an average speed of one body length per second. Some herring remain in inside waters near their spawning grounds throughout the year.

The stimuli that initiate spawning are not well understood. Spawning times are synchronized with water temperatures, and not until incubation temperatures are above 6°C do herring spawn in northern latitudes. However, adult herring may experience temperatures much lower than this just prior to spawning. In the western Bering Sea, sexually mature herring caught in late May in Olyotorskii Gulf entered through 0°C water into Korfu Bay to spawn (Kawamura 1971). In San Francisco Bay it has been observed that herring are more likely to spawn when the highest daily tide occurs during darkness (Spratt 1981). Recently, Brett and Solmie (1982) found that in impounded herring once the gonosomatic index reaches 24% of body weight, temperature was the prime determinant of spawning. Fish kept below 9°C failed to spawn during the course of the experiment.

In laboratory experiments it has been found that exposing mature herring to filtrates of ripe herring testes stimulated behavioral and physiological responses leading to spawning (Stacey and Hourston 1982). However, it is unclear whether male or female herring initiate spawning. Fraser (1922) observed that female herring deposit the eggs first followed by the male depositing the milt alongside. Regardless, it is probably true that once some male herring begin to spawn, this leads to

massive spawning of entire schools. Typically, most major spawns continue for several days and milt is distributed throughout the water where egg deposition occurs. Sperm density has been measured at 150 sperm/mL (Hourston and Rosenthal 1976a) at the sea surface, where sperm concentrations are considerably lower than at the bottom.

Both the male and female herring interact closely with the vegetation upon which the eggs are laid. The fish make ventral surface and genital papilla contact with the spawning substrate and deposit tracts of eggs and milt along its surface (Hourston et al. 1977). The texture and surface properties of the vegetation are tested by the fish prior to spawning, and sediment on the substrate may inhibit spawning (Stacey and Hourston 1982).

Atlantic Herring (*Clupea harengus harengus*)

Distribution of Stocks and Spawning Grounds

The Atlantic herring spawns both in the winter–spring and summer–autumn. The former spawns usually occur in shallow water, and in the northwest Atlantic these spawnings can be located by milty white water (Tibbo 1956a), similar to those of Pacific herring. This phenomenon is apparently not observed in the northeast Atlantic (A. C. Burd, pers. comm.). Fall spawnings usually occur in deep water, in which case the location of the grounds has been inferred from the distribution of ripe or spent fish, the catch of predators ("spawny" haddock), or the location and density of larval schools.

Consequently, there is some uncertainty about the exact location of some of the spawning grounds. The categorization of populations on the basis of properties of the life history, such as the inferred time and place of spawning, the fecundity and egg size, the maximum size and age, growth rate, and age composition, has provided a useful description of what are probably genetically distinct herring populations. The fecundity of spring spawners is considerably lower than for fall spawners and the eggs are larger (Hempel and Blaxter 1967; Hodder 1972). Some spring spawners also tend to grow larger and live longer than the fall spawners (Parrish and Saville 1965).

Northeast Atlantic spawners

Herring are known to spawn somewhere in the northeast Atlantic during every month of the year (Hodgson 1960). Most of these spawnings have been classified into what have become known as "winter–spring" (spawnings between January and May) and "summer–autumn" (spawnings between August and December). Cushing (1967) suggested that spring and fall spawners be divided into autumn, winter, and spring groups based on differences in spawning time and other biological characteristics. However, we restrict our discussion to the two groupings to limit confusion and retain consistency with the bulk of available literature.

Parrish and Saville (1965), following the early ICES subdivision (Parrish 1958), defined four groups of herring: oceanic, shelf, coastal, and some populations of *Clupea harengus pallasi*. Unfortunately, all but the last group contains both spring and fall spawning populations. On the basis of spawning time and locality, several dozen genetically distinct stocks may be present in the northeast Atlantic alone (Iles and Sinclair 1982).

For the purposes of management a much smaller number are generally recognized. Of these, one of the largest is the Atlanto–Scandian winter–spring spawning stock consisting of large fish that migrate off the continental shelf and whose spawning grounds encompass the west coast of Norway (Fig. 7) from the Lofoten Islands to the entrance of the Skagerrak (Runnstrom 1935; Devold 1963; Dragesund et al. 1980). The extent of its spawning grounds have decreased and the date of spawning delayed as the stock size has been reduced (Dragesund et al. 1980). Often grouped with this stock are the winter–spring spawners of Iceland (Fig. 8) off the south and west coasts (ICES 1979). There is also an Icelandic summer–autumn spawning stock occupying many of the same areas as the spring spawners (Einarsson 1958). The Faroe Islands also contain a winter–spring and summer–autumn spawning group, which is usually considered as part of the stock spawning off the south coast of Norway (Parrish and Saville 1965).

Adjacent to the British Isles are a substantial number of herring stocks that, although migratory, are restricted to shelf waters, primarily the North Sea (Fig. 8). They consist of both spring and autumn spawning fish although the latter have predominated since the early 1950's (Saville and Bailey 1980). Several identifiable fall spawnings occur off the west coast of Scotland among the Hebrides: St. Kilda, Barra, Skye. The major spring spawning in this area occurred along the northwest coast of Scotland proper (Baxter 1958) but is now apparently extinct. Extant spring spawning populations occur along the northwest (Donegal) and south coasts (Dunmore) of Ireland and in the Firth of Clyde (Parrish and Saville 1965; Hempel and Blaxter 1967; Malloy 1980). The Irish Sea also contains two autumn spawning stocks, the Manx and the Mourne herring (Bowers 1980).

The literature attempting to define the stocks in the North Sea proper is not of a concensus, and the recent fishery-induced changes make this task more difficult. The three recognized groups are the Buchan, Bank, and Dogger spawners (Parrish and Saville 1965; Zijlstra 1969). The first two groups are summer–autumn spawners, while the latter tend to be winter spawners. Saville (1971) described the Buchan group as spawning to the north and east of the Orkneys, the northeastern tip of Scotland proper (Clythness), the Buchan area, and offshore on Turbot, Aberdeen, Montrose, and Berwick east banks. More recently there appears to have been a shift northward off these banks onto the previously little used Shetland Islands (Burd and Howlett 1974; Saville 1971).

The Banks fish spawned historically on the Dogger Bank off the mideastern coast (Shields) of Britain (Cushing 1955; Burd and Howlett 1974). Since the mid-1960's the fish have not been spawning on the banks but have shifted offshore (ICES 1978).

The herring spawning in the southern section of the North Sea or Straits of Dover are known as the Downs fish and are sometimes divided into the Sandettie and Channel spawners (Parrish and Saville 1965). They differ from the other two groups in that they spawn later in the year, mid-November through mid-January (Cushing 1955, 1967). Several distinct spawning grounds have been delineated (Burd and Howlett 1974), although in recent years there has been a contraction in size and an apparent disappearance or shift of the Sandettie group towards the Channel grounds (ICES 1978).

Several small spring spawning stocks were known to exist in the North Sea at one time. The Firth of Forth and Plymouth spawners are now both apparently extinct (Saville 1963; Parrish and Saville 1965). The small stock in the Blackwater Estuary was thought extinct but appears to be returning (Dempsey and Bamber 1983).

The stocks spawning along the continental coast of Europe including the Baltic and White seas have been referred to as

FIG. 7. Herring spawning stocks and grounds of the northeast Atlantic. Month(s) of spawning indicated by two-letter abbreviations.

coastal spawners (Fig. 7). With the exception of the Baltic fish they apparently do not migrate very extensively. The separation of stocks at the entrance to the Baltic is particularly poorly understood (Rosenberg and Palmer 1982). They distinguish five groups: the Skagerrak and Kattegat spring spawners, the Kattegat coastal spring spawners, the Skagerrak Fjordic spring spawners, and the more or less extinct Kattegat autumn spawners sometimes known as the Kobbergrund stock. These fish all spawn along the Swedish west coast, the Oslo fjord in the Skagerrak, and among the islands down into the Kattegat. In addition, ICES (1978) distinguished a Jammer spring spawning stock in the Skagerrak and several small groups along the west coast of Denmark as far south as the Elbe Estuary.

The stocks of the southern Baltic are spring and fall spawners. Popiel (1958) described three groups in the western Baltic. A group of autumn fish occurs in the Bornholm–Rugen area extending as far east as the Gulf of Gdansk. On the west they meld with the stocks of the Kiel and Schlei Bays and the Kattegat stocks. The spring fish are concentrated in the Rugen area and Gdansk Bay. To the north are the spring spawners of Gotland and Oland and the eastern Swedish coast. These spawnings extend virtually around the entire Gulf of Bothnia and into the Gulf of Finland (ICES 1979).

Rannak (1971) distingushed among six groups of spring spawning herring in the eastern Baltic Sea. There is a stock at the head of the Gulf of Finland. This grades into a stock on the north and south shores of the western Gulf of Finland. South of this stock is the group of spawnings around the Hiiumaa–Vormsi Islands. Farther to the south is the Ventspils stock, which extends into the open Baltic on the west and into the Gulf of Riga on the east. On the north it extends into the Gulf of Parnu. This group overlaps with the Gulf of Riga stock. South of the Ventspils are the stocks of the Gulf of Gdansk mentioned earlier. The only autumn spawning in the eastern Baltic occurs in the Gulf of Riga (ICES 1979; Anokhina 1971).

The most northerly spawning of Atlantic herring occurs in the White Sea. The fish here are morphologically similar to Pacific herring and spawn both during the spring and summer (Soin 1971). Spawning occurs in the Gulfs of Dvina, Onega, and Kandalaksha (Tambovtsev 1959). The taxonomic status of these groups is unclear, as the Russian workers refer to them as a distinct subspecies (Soin 1971).

Northwest Atlantic spawners

The spawnings in this region also occur both in the spring and fall. At present, spring spawning predominates in the north,

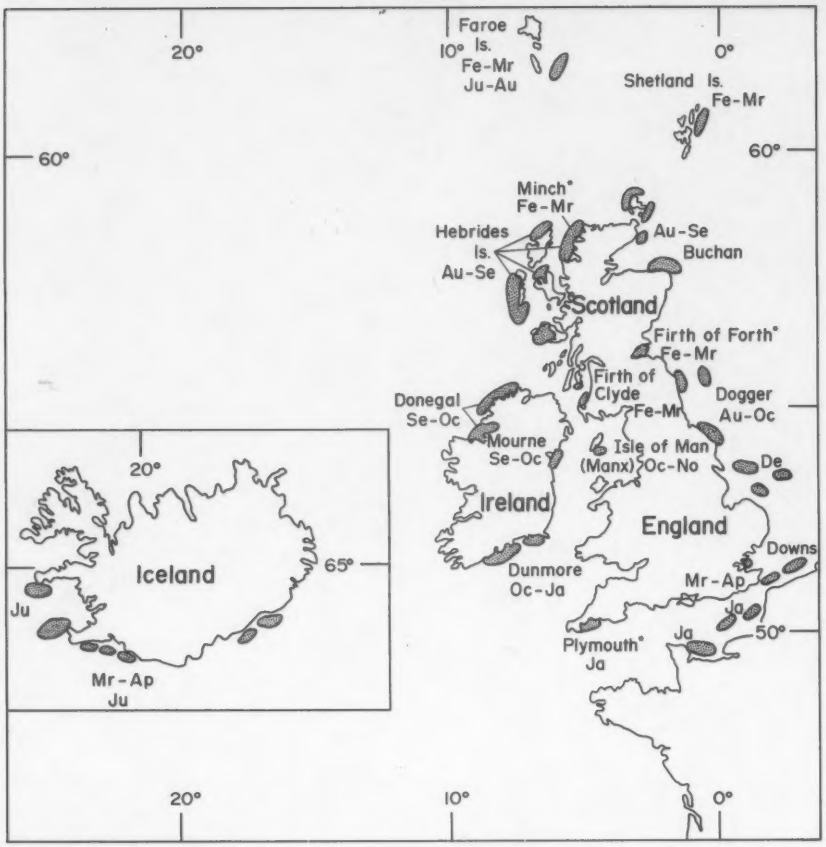

FIG. 8. Herring spawning stocks and grounds of the North Sea. Month(s) of spawning indicated by two-letter abbreviations. Asterisk indicates extinct population.

while fall spawning is prevalent south of the Gulf of St. Lawrence. Scattergood et al. (1959) indicated that the spawning range extends from northern Labrador as far south as Virginia. The northern range extends to the west coast of Greenland but it is not certain whether spawning occurs here (Bigelow and Schroeder 1953). However, spawning is known to occur on the Labrador coast predominantly as summer spawners, in July–August (G. H. Winters, pers. comm.).

Spawning occurs in all of the coastal bays of Newfoundland (Fig. 9). Several populations are recognized: Notre Dame Bay, Bonavista–Trinity Bay, Conception Bay–South Shore, Fortune–Hermitage Bay, Placentia–St. Mary's Bay, and the Newfoundland west coast, primarily St. George's Bay and Bay of Islands (Moores 1980; Tibbo 1956a, 1956b). Most of these areas contain primarily spring spawning populations (Parsons 1973).

The major autumn spawning population occurred along the southwest shore of Newfoundland prior to 1974. Since then, spring spawners have again become prevalent in this area (Moores 1980). Several authors have speculated that the fish overwintering in southwestern Newfoundland comprise the same stock of fish that spawns and feeds in the southern Gulf of St. Lawrence based on meristic and tagging data (Hodder and Parsons 1971a, 1971b; Parsons 1973; Lett and Kohler 1976; Winters 1976). However, Ware and Henrikson (1978) presented evidence that at least two distinct spring and fall spawning stocks and conceivably several exist in the southern Gulf of St. Lawrence. They have mapped out the myriad of localized spawning grounds along the southern Gulf of St. Lawrence from the southern Bay of Chaleur to Cape Breton Island. The majority of these spawnings are in the spring but fall spawnings occur at Miscou, Escuminac, North Point on Prince Edward Island, and near Pictou Island. The spawning at the Magdelan Islands occurs in the spring. Messieh (1975) indicated that fall spawnings occur along the west coast of Cape Breton Island and spring spawnings farther east in St. Anne's Bay. Jean (1956) described the spring and fall spawnings on the north shore of the Bay of Chaleur near Grande Rivière.

A number of small stocks occur along the north shore of the Gulf of St. Lawrence. Iles and Sinclair (1982) defined two, those at Île Verte and Anticosti Island. The latter is probably the Havre St. Pierre stock described by Day (1957). He suggested that the Île Verte spawners and those at Sept-Îles are one stock. Similarly, the fish at Matane, Fox River, and Havre St. Pierre appear to be a single stock. All these fish are spring spawners, although he mentioned a run of "Labrador" fall spawners that occur along the Gaspé and North Shore.

Off the northeast tip of Nova Scotia, Anthony (1972) and

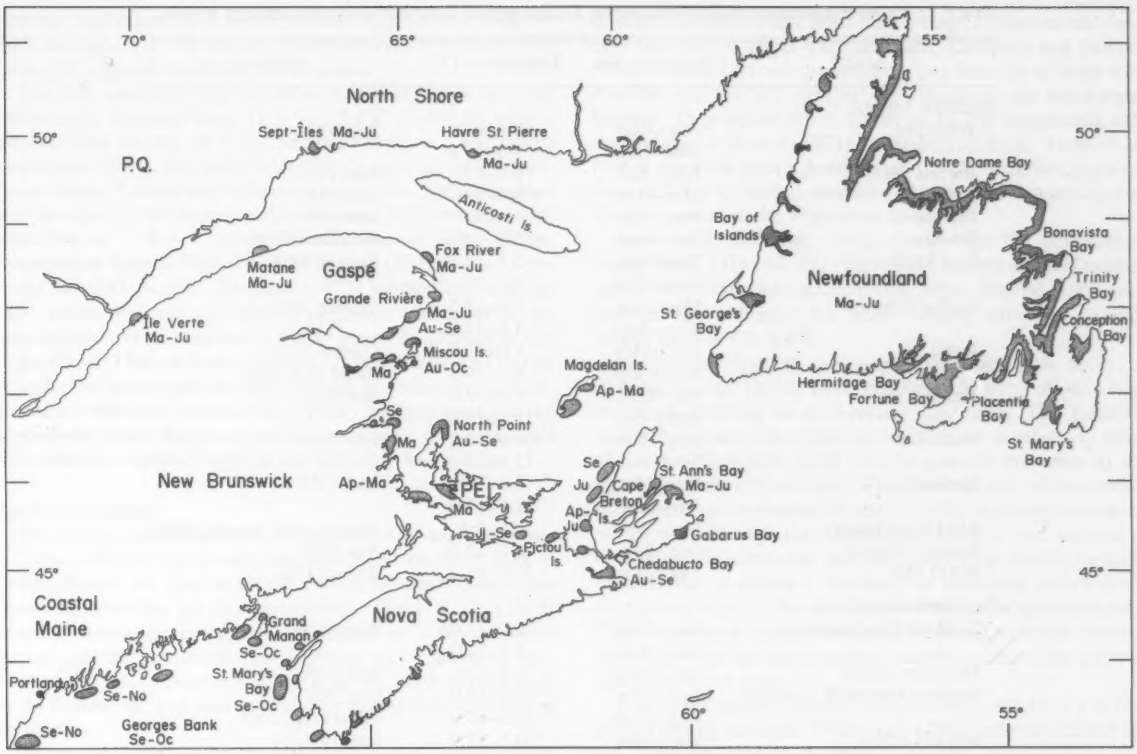

FIG. 9. Herring spawning stocks and grounds of the northwest Atlantic. Month(s) of spawning indicated by two-letter abbreviations.

Hodder and Parsons (1971b) referred to a Banquero and Canso Banks stock that probably are the fall spawners of Chedabucto and possibly Gabarus Bay (Parsons 1973). To the south of this group are a series of small spawnings along the southern half of Nova Scotia (Boyar et al. 1973) grading into the large spawning of St. Mary's Bay (Iles and Sinclair 1982; Das 1968; Anthony 1972). Anthony and Boyar (1968) distinguished two major spawning groups in the Gulf of Maine area. The first includes the Nova Scotia spawners mentioned above and the numerous small spawnings that occur from the west coast of the Bay of Fundy down through the Gulf of Maine roughly to the New Hampshire border. The other group consists of the spawnings in the Cape Cod area and the previously large spawning on Georges Bank. These are all fall spawnings occurring mainly in September through early November (Boyar 1968). Bigelow and Schroeder (1953) and Das (1968) reported that some small spring spawning stocks that spawned in April and May along the Nova Scotia side of the Bay of Fundy as far as Digby Gut and Parrsboro on the New Brunswick side were present at one time. It is not known whether these stocks still exist. They reported Block Island as the southern extent of spawning but any spawning south of Portland is negligible.

Spawning Ground Characteristics

The available data on Atlantic herring spawning grounds, although not extensive, suggest some similarities in the localities chosen by the fish for egg deposition. The spawning grounds are all in high-energy environments, either in nearshore shallows subject to wave and tidal flux for intertidal spawners or in tidally active areas for the deeper water summer–autumn spawnings (Rannak 1971; Drapeau 1973). Iles and Sinclair (1982) demonstrated a marked correspondence between known spawning grounds and the distribution of thermally well-mixed areas as determined by the Simpson–Hunter stratification parameter. This implies that spawning grounds occur in areas where the larvae will be retained under conditions favorable for feeding and growth, since these well-mixed areas have been found to sustain high levels of primary production. The temperature at which spawning occurs is remarkably variably (Table 1), ranging from 0°C in high-latitude spring spawnings to near 20°C in some fall spawnings. Similarly, salinity can range from virtually freshwater in the Baltic to 35‰ off the Norwegian coast.

Fall spawnings

Much of the information on the location of fall spawning grounds comes from indirect inferences such as the distribution of "spawny" haddock or ripening adult herring (Fridriksson and Timmermann 1951; Postuma et al. 1977). Similarly, most of what is known about the physical characteristics and density of deepwater herring spawns has been inferred from grab samples of various types of unknown efficiency. In fact, Tibbo et al. (1963) found that grab samples did not provide a reliable indicator of the spawn density, suggesting very light spawn when in fact it was 10–20 layers thick. The grab apparently did not sample seaweed efficiently either, retrieving only the stony substrate without the plant material. Given the shortcomings in the data it is surprising that the observations about deepwater spawning grounds are so consistent.

TABLE 1. Water temperatures during spawning for Atlantic herring in the northeast and northwest Atlantic.

Locality	Spawning time	Temperature (°C)	Reference
Northeast Atlantic			
White Sea	Apr.–May	−0.8–0.2	Soin 1971
	June–July	9.0–11.0	
Barents Sea	Feb.–Apr.	0.0–6.9	Jean 1956
Iceland	Mar.–Apr.	5.0–9.0	Jean 1956
Faeroes	Mar.–Apr.	~3.0	Jean 1956
Norway	Feb.–Mar.	5.0–6.0	Runnstrom 1941
East Baltic	May–June	2.5–17.5	Rannak 1959
	Aug.–Sept.	2.9–7.3	
Gulf of Riga	May–June	9.0–17.0	Ojaveer 1981
	Aug.–Sept.	7.0–12.0	
Baltic Sea	Apr.–May	5.0–13.0	Ojaveer 1981;
	Aug.–Sept.	8.0–16.5	Aneer et al. 1983
Kattegat	Jan.–June	4.0–12.0	Jean 1956
	Sept.–Oct.	11.0–13.0	
North Sea	Aug.–Nov.	6.0–13.0	Jean 1956
		12.0–14.0	
Scotland	Feb.–Mar.	3.9–7.1	Jean 1956
	July–Sept.	11.0–12.0	
Blackwater Estuary	Mar.–Apr.	4.4–5.4	Dempsey and Bamber 1983
English Channel	Dec.–Feb.	6.0–12.0	Jean 1956
Isle of Man	Aug.–Nov.	10.0–15.0	Bowers 1952
Northwest Atlantic			
Southern Newfoundland	May–June	2.0–12.0	Parsons 1973
	Aug.–Sept.	8.0–16.0	
Magdalen Islands	Apr.–May	3.8–4.5	Jean 1956
Southern Gulf of St. Lawrence	Apr.–June	3.0–10.0	Day 1957;
	Aug.–Sept.	9.0–19.0	Tibbo et al. 1963
Bay of Chaleur	May–June	0.5–12.9	Jean 1956
	Aug.–Sept.	10.0–16.6	
St. Mary's Bay, N.S.	Sept.–Oct.	11.3–12.0	McKenzie 1964
		7.0–9.5	Das 1968
Grand Manan, N.B.	Aug.–Sept.	7.1–11.1	Bigelow and Schroeder 1953
Cape Cod	Oct.–Nov.	11.7–12.8	Bigelow and Schroeder 1953
Georges Bank	Sept.–Nov.	11.9–13.9	Scattergood et al. 1959
Block Island Sound	Oct.–Nov.	13.0–15.0	Jean 1956

Ewart (1884) was the first to suggest that herring spawn on hard substrate and *Laminaria* sp. in deep water on Ballantrae Bank. He also indicated that divers found spawn preferentially deposited in hollow basin-shaped areas rather than on ridges. The spawn covered many square meters with a 1.5-cm layer of eggs. Hemmings (1965) confirmed these observations, also visually, and indicated that the eggs formed a continuous carpet over the bottom, being deposited on the crests of ridges, but not in the hollows on the sea bottom near the edge of the patch, suggesting that the ridges are preferred but as the spawn becomes denser the hollows also become filled in. Parrish et al. (1959) also reported on the spawning in a small area (1 km^2) 13–24 m deep on Ballantrae Bank. Spawn was continuous on small stones and gravel and of four to eight layers thickness. Virtually all the eggs were fertilized and very few were dead (<1%). Bowers (1969) reported two spawning beds (0.01 and 0.05 km^2) off the Isle of Man in 44 m of water on coarse gravel but also on fronds of *Glycymeris* sp. and *Flustra foliacia*. Bolster and Bridger (1957) found spawn attached to 2.5- to 25.0-cm-long flints in the Sandettie area of the English Channel covering an area 3.2 km long and 320–365 m wide. Rannak (1959) found that the fall spawnings in the Baltic occurred below 10 m on gravelly substrate at 14–16°C.

Iles and Caddy (1972) observed spawn from a submersible in 50 m of water on the northern edge of Georges Bank. It was deposited over a substrate of level gravel. They also reported sand waves of 10 m or more in height extending to within 25 m of the surface in the area. Caddy and Iles (1973) reported that spawn only occurred in level areas of small rounded gravel (2–10 mm in diameter). They also remarked that the spawning grounds had contracted in size from previous surveys with a decrease in spawning stock size. McKenzie (1964) reported a spawning bed of 0.07 km^2 off southwest Nova Scotia. Spawn was deposited primarily on flat substrate of sand and small stones as well as a dense growth of *Desmerestia aculeata*.

Drapeau (1973) suggested that the herring spawning on Georges Bank occurs in such a high-energy environment that it is imperative that the eggs be attached to a stable material such as gravel to prevent their translocation.

Densities of eggs observed on the spawning grounds are quite variable within areas but comparable between areas. In general, the density of spawn rarely exceeds 2 cm in thickness. Bowers (1969) reported egg densities in his grab samples of from 0.30 to 1.65 million eggs/m^2 with a maximum of about nine layers (1.25 cm) of eggs. Iles and Caddy (1972) found eggs in a uniform mat of 1–2 cm (approx. 7–14 layers) in thickness

roughly equivalent to 2.4–4.8 million eggs/m^2 (1 layer = 340 000 eggs/m^2). McKenzie (1964) reported 0.3–3 cm (2–4 layers) of eggs off southwest Nova Scotia.

The fall spawned eggs develop at a fairly high ambient temperature ranging from 11.3 to 12.0°C (Table 1) with a marked tidal current of 1.5–2 knots (1 knot = 1.852 km/h) (McKenzie 1964). Iles and Caddy (1972) reported tidal velocities of up to 3 knots and temperatures of 14–15°C associated with the Georges Bank spawnings. Bowers (1952) reported tidal velocities of 1.8–4.5 knots off the Isle of Man. Water temperature ranged from 10 to 15°C and salinity was in the range of 33.0–34.4‰. Drapeau (1973) pointed out that the tidal action not only provides oxygenation and prevents the accumulation of metabolites but also prevents siltation of the eggs. Ewart (1886) was able to hatch eggs in 98 fathoms (180 m) of water but those eggs that were covered by sediment had died. Bowers (1969) and Parrish et al. (1959) both reported that the eggs in the lower layers of dense spawn were less developed than those on exposed surfaces and probably less viable.

Spring spawnings

The spring spawnings tend to be located in shallow water (<20 m), often in protected areas such as the heads of bays or fjords. Hence, the data on spring spawns has often come from direct observations by the researchers. Tibbo et al. (1963) reported spawnings in the Bay of Chaleur in 1–6 m of water exclusively on vegetation (*Phyllophora* sp., *Laminaria* sp., *Furcellaria* sp., *Chondrus* sp., *Fucus* sp., and *Ascophylum* sp.). *Zostera* sp. was also present but not used as a spawning substrate.

Aneer and Nellbring (1982) reported a shallow-water spawning (0.4–11.0 m deep) in the Baltic Sea primarily on *Pilayella littoralis*, a filamentous brown algae, but also on *Fucus vesiculosus* and *Ceramium* sp. Again, all the eggs were on vegetation rather than bottom substrate. Rannak (1971) indicated the occurrence of spawning on Phaeophyceae and Rhodophyceae beginning at 3 m and shifting to 10–12 m over the 1.5–2 mo of spawning in the east Baltic. Soin (1971) reported that White Sea spawnings occur in sheltered coastal waters and bays in spring and summer. The bottom is hard, sandy, or stony with *Zostera marina* or *Fucus vesiculosus* vegetation. Spawning occurred from 0.5 to 5.0 m mainly on *Fucus* sp. but also on rocks.

The only well-documented deepwater spring spawnings occur off the coasts of Norway and Iceland. Runnstrom (1941) collected over 2000 grab samples off the coast of Norway over a period of 7 yr. Most of the spawn occurred in 20–80 m of water on rocks, stones, gravel, and sand although sometimes also on brown and red algae. Of the samples containing eggs only 9% were estimated at more than 1 layer and only 0.4% at more than 10 layers. One sample contained the equivalent of 25 layers of eggs. The average density of spawn estimated over the years of the survey was approximately 135 000 eggs/m^2. Runnstrom (1941) also noted that there was a greater proportion of dead eggs in the bottom layers of spawn. Fridriksson and Timmermann (1951) reported spawn at 50 m with a density of only 5–1650 eggs/m^2 in grab samples off the coast of Iceland. Rannak (1971) and Aneer and Nellbring (1982) found only single strand or small clumps of one layer thickness in the Baltic. Aneer et al. (1983) reported 362 500 eggs/m^2 in a more recent Baltic survey. Soin (1971) reported a mean density of 250 000 eggs/m^2 in the White Sea. He found about 35% of the billion eggs deposited in a 2000-m-long × 20-m-wide spawning died due to desiccation from tidal changes. Most of the dead eggs were in the upper intertidal zone. Dempsey and Bamber (1983) reported on two spawnings in less than 5 m of water with 456 100 and 170 300 eggs/m^2 on average in the Blackwater Estuary. They reported a mortality of 13.7% comparable with the findings of Baxter (1971) on Ballantrae Bank. Tibbo et al. (1963) reported spawn densities of 1.5–21.9 million eggs/m^2 from SCUBA-collected samples and indicated that density was directly related to the vegetation density.

Aneer and Nellbring (1982) found that the temperature ranged from 7.0 to 14.0°C (Table 1) at the bottom, and salinity was 6.5‰ with no tidal action for the Baltic. Rannak (1959) also reported that salinities for Baltic herring spawning grounds ranged from 3.4 to 6.4‰.

In summary, herring spawning grounds appear to occur, as Iles and Sinclair (1982) have suggested, in areas of good tidal exchange resulting in well-mixed conditions. The substrate does not appear to be critical provided that it is relatively clean of fine sediment that could prevent gaseous exchange by the eggs with their environment. Temperature and salinity conditions also do not appear to be critical to the successful spawning of herring although they determine the rate and success of embryonic development and hatching. Egg density is quite variable but indicates a tendency to distribute spawn fairly evenly over most of the suitable substrate in the spawning area. This would have selective value in ensuring maximal material exchange with the environment, thereby maximizing survival and hatching of eggs.

Two other factors, predation and storms, can have a severe impact on egg survival. Tibbo et al. (1963) estimated about 7% egg mortality due to flounder predation. Soin (1971) gave evidence that summer spawned herring eggs were the main diet item for sticklebacks during June in Kislaya Bay in the White Sea. Caddy and Iles (1973) estimated from photographs that about 8% of herring spawn on Georges Bank was eaten by a variety of predators.

Much larger quantities of spawn appear to be lost by storm action. Runnstrom (1941) reported 80 000 L of spawn being taken from a beach in Norway. Tibbo et al. (1963) noted that large quantities of spawn were cast ashore by storms in the Gulf of St. Lawrence.

Spawning Behavior

It is generally accepted that Atlantic herring migrate back and forth between their spawning and feeding grounds. The factors that trigger the onset of migration, homing to the spawning grounds, and initiate spawning itself are not well known. Blaxter (1958) suggested that feeding conditions, temperature, salinity, and light levels may influence the latter.

Messieh (1977) reported a significant relationship between water temperature and arrival of fish to the spawning grounds in the Gulf of St. Lawrence. Similarly, Berenbeim and Sigaev (1978) found significant correlations between peak spawning on Georges Bank and the temperature anomalies at 50 and 75 m during August, i.e. just prior to commencement of spawning. Runnstrom (1941) found that the salinity of the water of the Norwegian coast determines the migration of herring inshore. When the less saline Baltic water intruded onto the spawning areas, the fish moved off the grounds. He also indicated that herring moved onto the grounds at night and spawned over several weeks, with the oldest fish spawning first followed in a second wave by recruit spawners. Finally, de Groot (1980) has

suggested that individual spawning grounds in the English Channel have specific noise spectra, produced by currents shifting the sand and gravel, which herring home onto.

There is surprisingly little information available on herring spawning behavior (Blaxter and Holliday 1963; Blaxter and Hunter 1982). Most of what is known comes from direct observations of fish in captivity. In Atlantic herring, sexual dimorphism in spawning behavior was reported by Ewart (1884). His observations on spawning behavior were that the female stops, almost touching the substrate, and releases a ribbon of eggs, which adhere to the bottom. Several males form a circle around, and some 20–25 cm above her release short ribbons of milt 1–2 cm in length, which slowly settle towards the bottom in the vicinity of the ova. He also suggested that females spawn over 3 d, while the males take about twice that long. They found that towards the end of spawning, males are predominant on the spawning grounds. Holliday (1960a, 1960b) confirmed the observations on spawning behavior and also demonstrated that herring apparently use visual stimuli in the selection of spawning sites. He placed herring in a tank with two patterns on a smooth bottom of which the fish preferentially chose that simulating a gravel bottom. In addition, he found that the exclusion of light from the tank stopped spawning activity.

Only one in situ observation on spawning behavior has been reported for the Baltic (Aneer et al. 1983). They did not observe the apparently coordinated behavior described above. Instead, they indicated an almost random intermingling of males and females on the spawning grounds. However, they indicated that they were unable to follow individual fish throughout a complete spawning sequence. They were also unable to confirm the apparent substrate testing reported for Pacific herring although they did note that fish touched the bottom from time to time and did appear to prefer certain vegetation types as a spawning substrate. Speed of swimming was observed as 24 cm/s, about half the normal rate. Finally, they reported quivering by both males and females, yawning, and the release of air bubbles. The water was observed to become turbid as spawning progressed but not to the extent that it was observable at the surface in 5 m of water.

Discussion

It is remarkable that two species that have been so extensively studied remain so poorly understood taxonomically. In large part this results from the tremendous diversity in spawning times and locales we find in both species, making it difficult to identify genetically distinct units. Over the last few decades there have been significant changes in both the timing and location of spawnings in both subspecies. To some extent this can be explained by natural fluctuations in the apparent abundance of different spawning groups. However, if we accept that these individual spawns represent genetically distinct "stocklets" it is cause for some concern. In the Pacific herring where spawning is confined to the winter–spring period we have nevertheless witnessed a marked trend toward later spawning (Hourston 1980). In conjunction with this we have seen the disappearance, from their usual spawning grounds, of a number of early spawning "stocklets" (D. E. Hay, pers. comm.). Similarly, the Norwegian and the Buchan stocks have not only modified the places where they spawn but also have delayed their spawning (Saville 1971; Dragesund et al. 1980). Since herring have historically generally been fished on their feeding grounds where there is often a mixing of spawning groups, one would have expected the eventual demise of the least productive stocks (Ricker 1973). Whether the loss of this genetic diversity is crucial to the long-term evolution and survival of the species is unknown. Nevertheless, it seems clear that we have reduced the total productive capacity of these stocks. As such, a clearer understanding of the relative significance of the various spawning grounds to overall production as well as of the factors that determine why herring spawn when and where they do may provide some guidance on how to optimally utilize the available herring resources.

Atlantic and Pacific herring do not differ markedly in their choice of spawning grounds, the timing of spawning, and spawning behavior, the main difference being that the Atlantic herring spawning season is more protracted and that some summer–autumn spawners occupy considerably deeper water of a higher temperature during spawning. Food availability and limitation during the larval stage have been proposed as critical factors determining the survival and ultimate success of newly hatched herring larvae. Cushing (1967) was the first to present the relationship between the various spawning groups and peaks in plankton production in the northeast Atlantic. He also pointed out that the spawning time of various fish species including herring was fixed in time, which appears to be the best strategy to take advantage of an annually variable production cycle (Cushing 1972). It would then be the so-called "match or mismatch" of these processes that determined the ultimate year-class strength of the progeny of a spawning. Earlier, Colton and Temple (1964) and Stevenson (1962) had demonstrated that survival of newly hatched larvae was dependent on the retention of larvae in areas favorable for feeding and growth. Iles and Sinclair (1982) have subsequently shown a surprising coincidence of herring spawning grounds and vertically well-mixed, physically stable larval retention areas, which appear to determine not only the number of discrete spawning stocks but also their ultimate size. The high primary production and stability of the retention areas appear to be critical components in the high survival rate of the larvae. Hay and Fulton (1983) presented evidence that carbon from herring spawning products promotes secondary plankton production that could serve as food for emerging herring larvae.

From this, one can argue that evolution has favored the selection of spawning sites that place the larvae in an area favorable for their survival. The shallow-water spring spawnings generally occur in bays and inlets, which would not only act to retain larvae in the local environment but also the first vestiges of the spring plankton bloom are most apt to appear in these areas (Wyatt 1980). Similarly, the fall spawnings that occur in deepwater frontal zones place larvae in areas that are again going to retain the larvae in a localized environment with high production, which because of its well-mixed nature may remain actively productive over a somewhat longer period of time than the surrounding stratified zones. The disadvantages of inshore shallow spawning in the fall are the possibility of ice cover in high-latitude spawnings and increased storm probability. Also, Aneer and Nellbring (1982) indicated that much of the algae is in a state of dying and decay, which leads to deoxygenation and siltation, thus providing a poor substrate for egg deposition.

The match–mismatch hypothesis could also be seen as an explanation for the timing of herring spawns if spawning occurred at or just prior to peaks in plankton production. Unfortunately, Iles and Sinclair (1982) presented evidence that this does not appear to be the case for at least three tidally

energetic areas. Hence, an explanation for how the precise separation in timing of the various spawning runs is maintained is not clear. Recently, a number of authors have argued that competition and predation by Atlantic mackerel (*Scomber scombrus*) larvae, juveniles, and adults have had impacts on when and where herring spawn and also on ultimate stock sizes (Winters 1976; Lett and Kohler 1976; Ware and Henrikson 1978). The latter authors argued that herring spawning times appear to be structured in such a way as to minimize competition and predation by mackerel. Indeed, based on May and MacArthur's (1972) model of niche overlap, one finds that the seven herring spawning groups they identified in the southern Gulf of St. Lawrence are packed as closely as theoretically possible in terms of spawning time. Only the last spring and first fall group are separated more than expected. Interestingly, these two groups encompass the range of mackerel spawning, which suggest that competition by larval mackerel or predation by adult mackerel during their presence in the Gulf from late June through early August has precluded the survival of any more herring cohorts during this period.

The suggestion by Ware and Henriksen (1978) that predation by mackerel has led to disruptive selection in the seven separate herring spawning groups in the southern Gulf of St. Lawrence is intriguing but it is difficult to envision a mechanism that would lead to the observed diversity in spawning times given the relative constancy in mackerel spawning time (Ware 1977). We feel that the mechanism determining the spacing of herring spawning times is related to the growth rates of successive larval cohorts so as to minimize competition for food. That mackerel do impact on spawning time in a gross way is evidenced by the recent resurgence of dominance in the spring spawning herring in the southern Gulf of St. Lawrence coincident with the large increase in mackerel biomass during the late 1960's (Ware and Henrikson 1978). It appears then that the combination of different larval growth rates as determined by the local production cycles and predation effects determines the spacing in time of herring spawnings.

Unfortunately, comparable data are not available for the northeast Atlantic or Pacific to evaluate these arguments further. In several areas we do find two or more "waves" of Pacific herring spawners separated by 1–2 wk. It is conceivable that a more elaborate structuring of spawning stocks occurs here as well, and since there is no similar predator, selection for spawn timing would presumably result directly from intraspecific competition for food among the larval cohorts.

If such a stock structure has any basis in reality it implies an almost insoluble management problem. Herring are apparently relatively flexible in the locality they select for spawning, and although homing appears to occur in all stocks to some degree it is not to very precise geographical localities. Provided that suitable substrate is available in an adjacent area, spawning appears to occur successfully. Once eggs are deposited, fluctuations in temperature and salinity do not appear to affect egg development. Rather, most egg mortality appears to result from suffocation due to high egg densities and silting, predation, and, in intertidal spawners, from stresses imposed by exposure to air. Hence, recolonization of previously utilized spawning areas is conceivable and has apparently occurred in isolated instances (Dempsey and Bamber 1983). On the other hand, the timing of spawning appears to be finely tuned genetically so that the reestablishment of stocklets with unique spawning times may be impossible. The task of successfully managing several stocklets with staggered spawning times in adjacent localities while maintaining their genetic diversity presents both a perplexing and intriguing research problem.

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Factors Influencing Development and Survival of Pacific Herring (*Clupea harengus pallasi*) Eggs and Larvae to Beginning of Exogenous Feeding[1]

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The euryplastic Pacific herring (*Clupea harengus pallasi*) generally encounters temperatures ranging between 0 and 10°C throughout its distribution during the maturation and spawning of adults, incubation of eggs, and hatching of larvae. For many Asian stocks these events occur in the lower half of the temperature range; with North American stocks they tend to occur in the upper half of the range. In British Columbia waters, salinities associated with these events (range, optimum) are spawning (2.6–28.7‰, 27–28.7‰), ≥50% fertilization of eggs (4.5–42‰, 12–15‰), and maximum total hatch and hatch of viable larvae (4.5–42‰, 12–17‰). A low/low–high/high interaction between salinity and temperature also influences total hatch, hatch of viable larvae, and salinity tolerance of larvae. In addition, the following implications arise regarding aspects of the Pacific herring reproductive cycle, based on previously published and new data, and on speculative inference. The response of Pacific herring to salinity and temperature appears to have a commanding influence on the reproductive cycle and, thereby, on distribution of the species. Survival of eggs on substrate, related to respiratory activity, appears to be influenced by the transport and perfusion velocity of interstitial water in an egg mass. Such transport may involve perivitelline fluid colloid osmotic pressure; natural convection; the surge associated with wave action, beach slope, and depth; and possibly differences in resistance to convective flow of deoxygenated water from an egg mass based on orientation of the substrate. These relations would be modified by variations in deposition intensity (number of egg layers) and packing density (eggs per unit volume), and both factors may affect survival of occluded eggs in an egg mass differentially, depending on the substrate used. A review of data on salinity tolerance of herring larvae indicates that a variety of dosage-mortality techiques has been used, leading to noncomparable estimates of response. An assessment of upper incipient lethal salinities will require standardization of such techniques. Recent studies show that salinity tolerance of larvae is influenced significantly by salinity–temperature conditions during egg incubation. At usual incubation conditions in British Columbia waters, the upper boundary of larval tolerance is estimated as 27.5–31.7‰ S (72-h LC10). depending on incubation history. The fate of Pacific herring larvae carried into the higher salinities of offshore waters has been controversial. In the Strait of Georgia, British Columbia, substantial offshore dispersion of larvae occurs where surface conditions generally are 27–28.6‰ and 9–10°C in the early larval period. Although these salinities are near the upper boundary of salinity tolerance, larvae sampled in offshore waters (1981) had an apparent mean age of 15 d and were actively feeding and growing. From rates of disappearance of larvae in the offshore waters (9%/wk) and inshore waters (45%/wk) we conclude that usual surface salinities and food supply in the open waters of the Strait were not a dominant influence on larval survival. Assuming the larvae remain in the upper 10 m, we suspect their disappearance, at least offshore, to be largely the result of predation.

Dans l'ensemble de l'aire de distribution du hareng du Pacifique (*Clupea harengus pallasi*), poisson eurybiote, la maturation, le frai, l'incubation et l'éclosion des œufs se déroulent entre 0 et 10°C. Pour une grande partie des stocks asiatiques, ces étapes ont lieu à une température se situant dans la première moitié de cette plage, tandis que pour les stocks nord-américains, elle est plutôt dans la seconde moitié. En Colombie-Britannique on a mesuré la salinité des eaux (limites de la variation et valeur optimale) où se déroulement ces divers stades : frai (2,6–28,7 ‰, 27–28,7 ‰), fécondation des œufs ≥50 % (4,5–42 ‰, 12–15 ‰), éclosion totale maximum et éclosion de larves viables (4,5–42 ‰, 12–17 ‰). La salinité et la température, lorsqu'elles sont simultanément basses ou simultanément élevées, influent également sur l'éclosion totale, l'éclosion de larves viables et la tolérance des larves au sel. L'examen de données nouvelles ou déjà publiées et l'extrapolation nous apportent les renseignements suivants au sujet du cycle

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de reproduction du hareng du Pacifique. La réaction de ce poisson à la température et de la salinité de l'eau semble avoir un effet déterminant sur le cycle de reproduction et, dès lors, sur la distribution de l'espèce. Le taux de survie des œufs sur le substrat, en rapport avec l'activité respiratoire, semble déprendre du déplacement et de la vitesse de perfusion de l'eau intersticielle dans la masse d'œufs. Le déplacement de l'eau peut être lié à la pression osmotique dans le colloïde périvitellin, aux courants de convection naturels, au reflux créé par les vagues, à la profondeur et à l'inclinaison de la plage et peut-être même à la différence de résistance contre le courant de convection de l'eau désoxygénée qui s'écoule de la masse d'œufs selon l'orientation du substrat. Ces relations changeraient suivant l'intensité (nombre de couches d'œufs) et la densité (nombre d'œufs par unité de volume) de la ponte, deux facteurs pouvant influer de différentes façons sur la survie des œufs du centre de la masse, selon la nature du substrat. L'examen des données recueillies sur la résistance des larves au sel révèle qu'on a employé des méthodes et des doses différentes pour étudier cette question, si bien qu'il est impossible de comparer les résultats obtenus. Il faudra uniformiser ces techniques pour déterminer la valeur initiale supérieure de la salinité létale. Selon des études récemment effectuées, la tolérance des larves au sel dépend dans une mesure significative de la salinité de la température de l'eau durant l'incubation des œufs. En Colombie-Britannique, en conditions normales, la limite supérieure de la tolérance des larves est estimée à 27,5–31,7 ‰ S (CL10 à 72 h), tout dépendant de l'évolution de l'incubation. On ne s'accorde pas sur ce qu'il advient des larves transportées jusqu'au large, dans des eaux de salinité accrue. Dans le détroit de Géorgie (C.-B.) on a constaté que durant la première partie du stade larvaire, bon nombre de larves se dispersent au large, là où général la salinité des eaux de surface est de 27–28,6 ‰ et la température de 9–10°C. Bien que cette valeur soit proche de la limite supérieure de la tolérance au sel, les larves échantillonnées au large (1981) étaient apparemment âgées de 15 jours en moyenne et elles se nourrissaient et se développaient activement. D'après le taux de disparition des larves dans les eaux du large (9 %/sem) et dans les eaux littorales (45 %/sem), nous avons conclu que dans le détroit de Géorgie les conditions normales de salinité et d'abondance de ressources nutritives dans les eaux de surface du large n'ont pas d'effets majeurs sur la survie des larves. En supposant que celles-ci demeurent dans une couche de 10 m à la surface, il nous semble possible que leur disparition, du moins au large, soit en grande partie due à la prédation.

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In the past 75 yr much has been learned about the variables that determine year-class strength of Atlantic (*Clupea harengus harengus*) and Pacific (*C. harengus pallasi*) herring, characteristics of their populations, and factors that influence fecundity and reproductive success. Biological–environmental relations have been examined regarding the spawning approach of adults, the timing of spawning, location of spawning grounds, the incubation environment, availability of suitable larval food, growth, and the impact of predation on larval survival. Yet, as Blaxter and Hunter (1982) comment in their review of clupeoid biology, "The Atlantic and Pacific herrings [remain] one of the most enigmatic biologically." Uncertainty of the specific or subspecific status of the two forms confirms this view. Statements of these authors provide the following perspective.

> The timing of reproduction in marine fishes is believed to have evolved as a mechanism to synchronize the occurrence of larval stages with the optimal phase of the annual plankton production cycle. As the spawners must depend predominately on indirect signals (photoperiod and temperature) to link the production cycle to spawning the chance of a mismatch ... may be large and failure to achieve a match may be a determinant of year-class strength. ... we do not understand what environmental variables determine the onset and cessation of spawning in the sea ... a certain temperature history prior to spawning, food supply and possibly day length are [concluded to be] important. More recent information supports this view.
>
> Selection of the optimal period for peak spawning is probably controlled by larval food habits, growth rates of larvae and juveniles [and] seasonal changes in the structure of zooplankton populations. ... The season and time of day of spawning, spawning habitat, size of eggs and density of spawn all may affect the survival of eggs and larvae.
>
> The remarkably shallow habitat used by the Pacific herring may be a way of maintaining the eggs and larvae in the nearshore zone. ... It appears that the chief benefit of demersal spawning is the production [and concentration?] of larvae in a very specific region at a very specific time. ...
>
> It is generally thought that disease, parasitism and inimical environmental conditions of temperature, salinity or oxygen are of minor importance in mortality [and that] the main causes of mortality are starvation and predation in the early pre-recruit stages. ...

Given the current state of knowledge, it is difficult to quarrel with these views. Similarly, one cannot fix attention on a given stage in the life cycle without acknowledging that all stages to some degree are interdependent regarding the biological and environmental factors that affect them. Hence, optimum conditions for egg incubation likely are related to factors governing selection of spawning habitat by the adult. Nor can there be a distinct analytical division between physical and biotic variables, such as temperature and food supply, that influence larval survival.

From numerous studies we conclude that the Pacific herring and its embryonic and larval stages essentially are euryplastic. Behavioural attributes of the adult spawner in selecting the spawning site, and compensatory mechanisms in the egg and embryo regarding the incubation environment, apparently combine to set the probability of hatching success, after which larval survival is largely dependent on timing in relation to predation and food supply. We propose here to examine some of the variables influencing survival and development, particularly salinity and temperature, between egg fertilization and beginning of external feeding in Pacific herring, some experimentally determined adaptive capacities of embryonic and larval stages, and how these capacities are utilized ecologically.

TABLE 1. Field observations of salinity and temperature levels associated with spawning approach, spawning, and experimental estimates of levels associated with egg incubation and early larval survival and development. In some instances, estimates of bivariable optima are shown; in others, an optimum in one variable (e.g. salinity) may be shown at a specific level of the other variable.

Characteristic	Salinity (‰)			Temperature (°C)		
	Range	Optimum	Source[a]	Range	Optimum	Source[a]
Approach						
Russian waters	—	—		<0–10.7	3–9	1
Maximum	—	—		8–10	—	1
Japanese waters	—	—		4–6	—	2
Spawning						
Canada, Pacific coast	8.2–27.7	—	3	5.8–10	—	3
Canada, Pacific coast	2.6–28.7	27–28.7[13]	4	—	8–8.9[b]	4
Canada, Pacific coast	—	—		—	7–8	5
Canada, Pacific coast	—	—		5–10	—	6
Russian waters						
Pacific	14–35	—	7	0–10	—	7
Barents Sea	25–31	—	7	3–12	—	7
White Sea	5–27	—	7	0–10	—	7
Japanese waters	17.4–18.5	—	8	—	—	
Incubation						
Fertilization ≥50%	4.5–42	10–20	9	~6.5–7.0	—	9
Fertilization ≥50%	10–30	12–15	9	~7.0	—	9
Max. capsule strength	10–28	—	10	—	—	
Max. capsule strength	>20	—	4	~5.0	—	4
Max. salinity tolerance	11.5–16.2	—	3	—	—	
Max. osmotic scope	13.2–19.0	—	4	~5.0	—	4
Max. total hatch	—	12.0	11	—	6.5	11
≥50%	4.5–42	17.0	9	~6.5–7.0	—	9
Max. viable hatch	10–24	17.0	11	6.5–10.5	8.3	11
≥50%	4.5–42	17.0	9	~6.5–7.0	—	9
Larvae						
Max. length at hatching	≤17	—	9	~7.0	—	9
Max. length at hatching	—	20.0	11	—	5.5	11
Max. length at hatching	~13, 21, 29	~13	12	~6, 12	~6	12
Max. growth·d^{-1} (on yolk)	~13, 21, 29	~21	12	~6, 12	~12	12
Min. calories growth·increment^{-1}·d^{-1}	~13, 21, 29	~13	12	~6, 12	~12	12
Max. salinity tolerance	6.1–34.3	—	3	—	—	
Max. salinity tolerance	>5–<20		4	~8.5	—	4
72-h LC50 (lower, upper)	5.2–33	—	4	~8.5	—	4
72-h LC50 (upper)[c]	34.2–51	—	12	~6, 9, 12	—	12
72-h LC10 (upper)	<20–33.5	—	4	~8.5	—	4
72-h LC10 (upper)[c]	22.3–39.3	—	12	~6, 9, 12	—	12

[a]Sources: 1, Svetovidov (1952); 2, Motoda and Hirano (1961); 3, McMynn and Hoar (1953); 4, Alderdice et al. (1979a); 5, Outram (1955); 6, Kasahara (1961); 7, Dushkina (1973); 8, Kurata (1959); 9, Alderdice and Velsen (1978); 10, Galkina (1957); 11, Alderdice and Velsen (1971); 12, Dueñas (1981).

[b]Modal values.

[c]Influence of incubation salinity and temperature on salinity tolerance of newly hatched larvae.

Influence of Salinity and Temperature on the Reproductive Cycle

A number of field and experimental observations of salinity and temperature associations with the reproductive cycle are summarized in Table 1. In Asian waters of the North Pacific Ocean the spawning approach occurs predominately at temperatures of 0–10°C. Such data are sparse for British Columbia waters, although approach to the spawning grounds and spawning would occur largely in the upper half of the 0–10°C range. In British Columbia waters, herring spawn within a broad range of salinities (2.6–28.7‰), although modal spawning salinities are noted as 27–28.7‰ at 7–9°C. The upper limit for natural spawning of stocks of commercial size in North American waters is about 10°C (Alderdice and Velsen 1971). Incubating eggs also tolerate a wide range of salinities and temperatures. Salinities providing 50% or greater fertilization, total hatch or hatch of viable larvae, range from 4.5 to 42‰ (Alderdice and Velsen 1978) at temperatures of 6.5–10.5°C, with substantial hatches occurring at least to temperatures of 14°C (Alderdice and Velsen 1971). Optimum fertilization salinities are 12–15‰; those for incubation success are 12–17‰ at 6.5–8.3°C. There is also a low/low–high/high interaction between salinity and temperature (Fig. 1) that influences

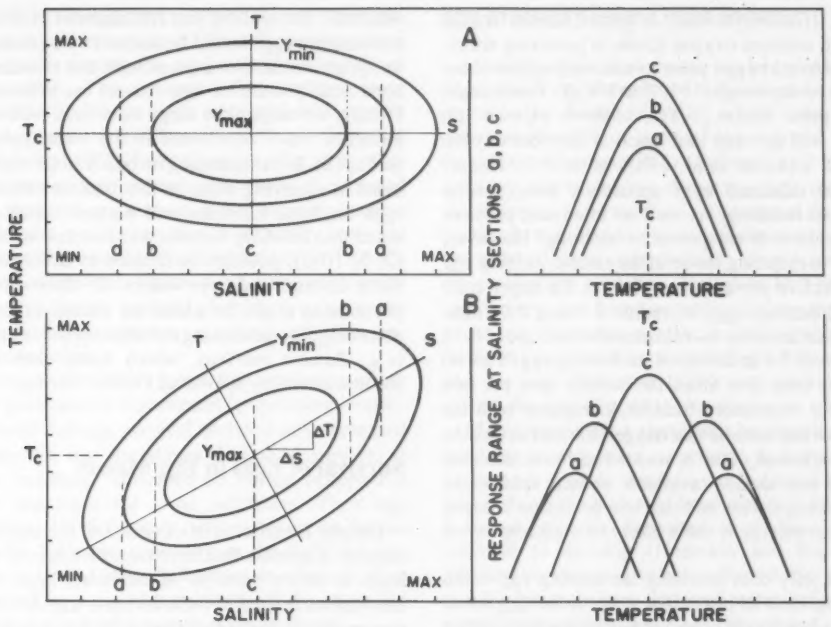

FIG. 1. Stylized response surface, assumed to be elliptical, illustrating the influence of a low/low–high/high interaction (B, left) between salinity and temperature, compared with a similar surface but no interaction (A, left), on the temperature range available to the organism (right). The surfaces shown, with major (salinity) axis S, minor (temperature) axis T, common S,T at the surface centre Y_{max}, and minimum response at the peripheral isopleth (Y_{min}), differ only in the counterclockwise rotation of the axes (B, left) around the surface centre. Hence, where the interaction occurs, a salinity change (ΔS) is coupled with a temperature change (ΔT) to retain a locus on the salinity axis. Sections a, b, and c through the response surfaces (left) are approximated (right). In A, the three sections have a common temperature (T_c) at their centres on the S-axis. In B, centres of sections a, and b are displaced from T_c by ΔT in relation to ΔS. Hence, the temperature range available to the organism is greater in B than in A (right). (While the argument stands, the temperatures of maximum response in each section (B) in fact are those for which $dY/dT = 0$; in addition, the resulting distributions (B, right) are skewed.)

embryonic and larval development. Hence, within the optimal ranges, lower salinities are coupled with lower temperatures and higher salinities with higher temperatures in relation to maximum incubation success. Early larvae also appear to be eurytypic. Length at hatching, larval growth rate, and growth efficiency on yolk appear high at salinities of 13–21‰ at temperatures between 5.5 and 12°C (Alderdice and Velsen 1978; Dueñas 1981). Larval resistance to higher salinities 0–9 d after hatching seems variable. Lowest mortality in unfed larvae occurred at salinities of 5–20‰. Three-day (72-h) LC50[2] and related estimates place the lower and upper larval salinity tolerance boundaries at 5–6 and 33–51‰, respectively. Dueñas (1981) has demonstrated that much of the variation in the upper range (33–51‰) can be explained by differences in salinity–temperature history during egg incubation. The implications of this finding will be outlined in a later section.

Respiration of Eggs on Substrate

Pacific herring deposit their eggs on aquatic vegetation in the sublittoral zone. Distribution of eggs is dependent on the type of vegetation available and the slope of the beach (Humphreys and Hourston 1978; Haegele et al. 1981). Intensity of deposition varies with respect to the bladelike, foliose, or filamentous nature of the algal species present, and eggs are deposited at greater depths as the beach slope increases. Spawn also is found frequently on cobble, boulders, and rock faces. Deposition intensity is estimated as the number of layers (0.1–10 or more) of eggs attached to the substrate (Humphreys and Hourston 1978).

The delivery of oxygen to and removal of metabolites from eggs incubating under such conditions is pertinent to survival, particularly for occluded eggs in the interior of a clump or egg mass. We assume that substantial movement of water is required through the interstices between eggs in a mass to provide for respiratory exchange. At a salinity of 15‰, 8°C, Braum (1973) found that Atlantic herring eggs required at least 20% of oxygen saturation (~ 2.10 mg/L) in perfusing water, throughout development, to hatch successfully. Braum's eggs also reached a plateau of oxygen uptake of 7 $\mu L \cdot 100 eggs^{-1} \cdot h^{-1}$ (0.097 $\mu g \cdot egg^{-1} \cdot h^{-1}$) several days before hatching at an ambient oxygen level of 10.49 $mg \cdot L^{-1}$. Assuming similar respiration rates in Atlantic and Pacific herring embryos, and that the dry weight of a newly hatched Pacific herring larva is about 0.14 mg of which 30% is yolk (Dueñas 1981), Pacific herring embryos prior to hatching would use about 970 $\mu g\ O_2 \cdot g$ embryo dry $weight^{-1} \cdot h^{-1}$. Comparison is made with embryos

[2]Level of an environmental variable resulting in 50% mortality in a sample after an exposure period of 72 h.

of Pacific salmon (*Oncorhynchus*), a genus known for its requirement of high ambient oxygen levels in perfusing water. Coho salmon (*O. kisutch*) eggs prior to hatching utilize about 1220 $\mu g\ 0_2 \cdot g$ embryo dry weight$^{-1} \cdot h^{-1}$ at 8°C (P. Rombough, Pac. Biol. Stn., pers. comm.). Yet, chinook salmon (*O. tshawytscha*) eggs will develop and hatch at ambient oxygen levels of 2.5 $mg \cdot L^{-1}$ (Silver et al. 1963) at 11.0°C. Hence, Pacific herring and salmonid eggs apparently have similar uptake rates prior to hatching, as well as minimum ambient oxygen levels that allow development to hatching. However, delivery of oxygen to respiring tissue of the smaller herring egg would be more effective per unit time than in the larger coho egg. For coho and herring eggs of radius 3.9 and 0.74 mm, respectively, their surface area-to-volume ratios are about 0.77 and 4.1, a ratio of over 5:1 in favour of the herring egg. That is, the herring egg has over five times the surface area per unit volume of tissue for respiratory transfer, compared with the coho egg. Hence, we can assume that oxygen transfer across the capsule is highly efficient, that a somewhat lower ambient oxygen level than that usually available should sustain the gradient to the respiring tissue, and that low perfusion velocity of water moving past the egg is more likely to limit respiration in occluded eggs.

Thickness of the jelly coat investing the herring egg could influence the volume flow of interstitial water in an egg mass. As well, the extent of jelly coat cohesion between neighbouring eggs could reduce the effective respiratory surface of the egg capsule. The jelly coat becomes progressively thinner throughout incubation in relation to salinity level. In low salinity (5‰) the coat remains viscous and thick, it thins progressively at 20‰, and becomes a very thin sheet easily peeled from the capsule at 35‰ (Alderdice et al. 1979b). Hence, in salinities of 20‰ or greater the interstices between eggs (percent open space) in a clump of eggs would tend to increase with embryonic development, a tendency that could permit greater volume flow at higher oxygen utilization rates in later development and counteract the possible limiting effect of lower oxygen saturation levels at higher salinities. Yet Taylor (1971), who exposed Pacific herring eggs to incubation salinities of 10, 20, and 30‰ at various deposition intensities, found survival higher in the lower salinities. The results suggest a reduced tolerance of the eggs to higher salinities (30‰), which would be expected, and a compromise between salinity tolerance and factors influencing respiratory exchange at salinities somewhere below 30‰.

Respiration of eggs within an egg mass is assumed to require continuous movement and replacement of interstitial water. Several phenomena are assumed to be involved in water and oxygen transport to herring eggs. First is an efficient process for exchange across the capsule between perivitelline fluid water and interstitial water resulting from a relation between hydrostatic (internal egg) pressure and the perivitelline fluid colloid osmotic pressure (Alderdice et al. 1984). The gradient involved (effective filtration pressure) appears to allow a continuous, rapid, cyclic renewal of perivitelline fluid water, and presumably its dissolved oxygen, in teleost eggs. The second phenomenon, natural convection (O'Brien et al. 1978) in the microenvironment surrounding a respiring egg, is the tendency for deoxygenated water to flow by gravity because of its increased density. With incubating salmonid eggs the velocity of naturally convected water is about 75 $cm \cdot h^{-1}$. A third factor, which could enhance physical exchange of intersticial water, is the growth habit (upright blade or flat thallus) and position in the water column of the aquatic vegetation to which the eggs are attached. The sinking and replacement of deoxygenated water surrounding eggs would be assisted by a greater head difference on upright surfaces compared with that associated with the more horizontal posture of egg masses on bottom rock or rubble. Finally, we suspect the surge associated with wave action could influence water movement in the water column at depths to perhaps 5–10 m depending on beach slope and wave height, and assist in renewing water in the microenvironment surrounding eggs on fixed substrate and bottom material. Taylor (1971) noted that hatching success was reduced with increasing depth (0, 5, 10 m), possibly in relation to decreasing motion of the water column in deeper waters. To these circulation-inducing phenomena might be added the photosynthetic activity (CO_2-absorbing, O_2-generating) of chlorophyll-containing sea grasses (e.g. *Zostera marina*), which forms part of the vegetative substrate used by spawning Pacific herring.

Survival of Eggs in Egg Masses

Despite facilitation of oxygen and metabolite transfer in egg masses, it appears that increased thickness of spawn deposition leads to lower survival of occluded eggs. A compensatory mechanism related to reduced mass transfer of oxygen in such circumstances is the fact that occluded eggs may develop more slowly (D. E. Hay, Pac. Biol. Stn., pers. comm.). As peripheral eggs tend to hatch prior to occluded eggs, the latter may compensate by reducing rate of development in response to reduced oxygen supply. However, numerous field observations indicate that hatching of even moderately heavy spawnings virtually all takes place within a few hours. This would suggest that the occluded eggs either suffer little repressed development or they hatch at a less developed stage than their exposed counterparts. Spawning intensity, the number of layers of eggs deposited, varies within and between species of vegetative substrate. Layers of 4–6 eggs are not unusual; very heavy intensities may involve 12 or more layers. Furthermore, packing density, the number of eggs per layer, varies with substrate type, some substrates incurring a closer packing density than others. Hence, there may be substantial variability in the relation between survival potential of eggs and deposition intensity as influenced by differences in packing density. Taylor (1971) noted that "medium" deposition intensity (4–6 layers) resulted in less than maximum hatching success but did provide maximum larval production per unit area of spawn deposition. Taylor used both naturally spawned eggs on substrate and artificially molded egg masses at deposition intensities between 1 and 16 layers. Hatching success in molded masses was lower than that in natural clumps of eggs with the same number of egg layers. An examination of Taylor's (1971, p. 38) data is instructive. Relative larval production per unit area of spawn deposition was 1.0, 1.8, 3.0, 1.8, and 1.4 for spawn intensities of 1, 2, 4–6, 8–10, and 12–16 layers, respectively. Overall hatching success in the series was 100, 90, 60, 20, and 10% for the five spawn intensities. Modelling these relations, we find them applicable to ribbonlike, cylindrical or half-cylindrical egg masses. One may consider a strip of eggs deposited on both sides of a *Zostera* blade, the depostion in cross section consisting of layers in a hexagonal array. The outer peripheral layer of eggs, unoccluded, is assumed to be not subject to hypoxial risk. In a cross section of such an array of 5 layers, about 40% of the eggs are peripheral. The remaining 60%,

occluded by 1 to 4 layers of eggs, are assumed to be at some risk. If hatching success in such a mass is to follow Taylor's estimate of 60%, then mortality among the occluded layers would of necessity average 66%. This estimate of mortality among occluded eggs appears to be too large compared with current evidence relating egg survival and deposition intensity in nature (Hourston and Rosenthal 1981). It would appear that some other factor is involved that raises hatching expectancy of occluded eggs in naturally spawned egg masses. Since hatching success of molded egg masses was lower than in naturally spawned masses, we suspect differences in packing density in Taylor's data affected observed survival. That is, we assume in naturally spawned masses that lower packing density favours water movement and respiratory exchange, resulting in higher survival among occluded eggs.

Indeed, Hourston et al. (1984) found that hatching success varied among 14 substrates at 5 comparable spawning intensities. They also found that egg survival declined with increased spawning intensity but that the abrupt decline in survival at intensities above "medium," observed by Taylor, occurred at lower or higher intensities for some substrates. Their egg survivals ranged from 100% for very light spawning on the sea grass *Zostera* to 8% for heavy spawning on the leafy red alga *Rhodymenia*. Presumably, these differences in survival were related to differences in the packing density of the eggs, but related data on this subject have not yet been analysed.

Under usual conditions in Canadian waters, the adverse effect of dense spawnings on the production of herring appears to be limited mainly to the egg stage. Hourston et al. (1984) found variation in viability of Pacific herring larvae to be extremely small over a wide range of spawning intensities. However, Galkina (1971) found large numbers of nonviable larvae in hatchings from the Barents Sea and Sea of Okhotsk, which may have resulted from denser spawnings (up to 20 layers) or stress from less favourable environmental conditions.

From these considerations, spawning behaviour of Pacific herring appears to optimize egg survival through selective patterns of egg deposition. Fish of either sex test the available substrate for suitable rigidity and texture as part of a multistage ritual of spawning behaviour (Stacey and Hourston 1982). Preference for moderate rigidity and a smooth surface would lead to selection of upright vegetation, rather than less rigid types that lie on the bottom as well as vertically inclined rock and other nonliving surfaces. Eggs deposited on the preferred vegetation types tend to be more loosely packed; hence, they are subject to a higher rate of water exchange across their surfaces because of the upright stance of the vegetation and its movement within the water column. Moreover, the practice of the female of laying less than 50 eggs in a ribbon with each act of egg deposition (Hourston et al. 1977), and in avoiding overlaying egg depositions, would limit the depth of egg depositions to less than 5 layers. After the preferred substrate(s) has been fully utilized, there appears to be a change in spawning behaviour wherein eggs are released freely into the water column. These eggs settle to form a blanket on the bottom and on previously used vegetation (Hourston et al. 1977). Broadcast spawning behaviour would tend to maximize the relative production of viable eggs when the abundance of spawners is low to moderate, and reduce relative production progressively as the abundance of spawners exceeds available substrate. The resulting upper limit in total larval production for an individual spawning ground presumably could act to reduce feeding competition as a potential factor in year-class strength.

Egg Mortality from Other Sources

Mortality from other causes can be quite high during the egg stage. Major egg depositions in the intertidal zone frequently are exploited by flocks of gulls, which have been observed to consume 40–60% or more of the exposed eggs within 3 d of deposition (Outram 1958). Subtidal egg depositions are fed upon by diving ducks. Although their rate of consumption would appear to be much less than that of the gulls higher up on the beach, they also tear loose quantities of egg-laden vegetation and most of these eggs probably do not survive as a result of desiccation and predation. However, bird predation on herring eggs is irregular. Some spawnings escape the attention of birds, which may be feeding nearby, in some or all years. Variations in the timing and location of spawnings of the various stocks from year to year (Hourston 1980) may provide some protection against the loss of eggs to this source.

Major storms are a significant but erratic source of egg loss, resulting in egg-laden vegetation being torn loose by wave action and piled in windrows that extend for miles along the beach above the high tide level (Outram 1955). Some of these loosened eggs are deposited in shallow water, where they continue to develop (Hourston and Rosenthal 1976), but hatching success is adversely affected. Because Pacific herring usually spawn in very sheltered waters, the instances of major mortality from this source are limited and its overall effect on production probably is less than that of predation. Storm damage tends to be greatest in shallow water. Hence, under storm conditions at exposed spawning locations, extension of spawning into deeper waters where other conditions for egg survival are less promising may provide some net survival advantage.

Salinity Tolerance in Hatched Larvae

Stevenson (1962) concluded that survival of Pacific herring larvae passively transported into the open waters of the Pacific Ocean could be limited by their inability to tolerate higher offshore salinities. Accumulated evidence does suggest that survival and development of Pacific herring eggs and larvae are favoured within a salinity range of 10–30‰ and that optimal salinities are approximately 10 to 20–21‰ (Table 1). The literature also indicates that no clear distinction has been made between salinity tolerance and salinity resistance. Following Fry's (1947) concept, salinities within the zone of tolerance are those an organism may withstand "indefinitely," while survival or normal function within the zone of resistance is limited by the level of salinity imposed and the time of exposure. Between these zones is an incipient lethal response boundary. The boundary may be estimated as the salinity at which lethal exposure time becomes infinitely long in 50% of a group of test larvae. The location of the boundary may be modified by acclimation, or prior physiological experience of the organism. To our knowledge this concept has not been applied to the estimation of salinity tolerance in herring larvae. Furthermore, those reported measures of resistance to higher salinities, beyond the incipient lethal boundary, have employed various periods of exposure ranging from approximately 1 to 20 d (Table 2). Assuming for the moment that salinity resistance remains constant over the test period, then in a series of salinities, declining median lethal (LC50) salinities would be obtained with increasing exposure times until an asymptotic level is approached at some extended exposure interval.

TABLE 2. Estimates from the literature of upper LC50 salinities (‰) over test intervals of 1–19 d in samples of Pacific herring larvae 1–20 d old at end of test period.

Age of larvae at end of test (d)	LC50 (‰) for test intervals (d): 1	2	3	5	7	19
1	42.1[a.1]	—	—	—	—	—
2	—	42.1[a]	—	—	—	—
			35.5[b]			
3	—		39.0[c.1]	—	—	—
			48.2[c.2]			
5	—	—	—	41.9[a]	—	—
6	—	—	36.5[b]	—	—	—
7	—	—	—	—	37.0[a]	—
9	—	—	42.5[b]	—	—	—
10	55.0[a.2]	—	—	—	—	—
12	—	—	35.5[b]	—	—	—
19	—	—	—	—	—	33.5[a]
20	38.3[a.3]	—	—	—	—	—

[a]Kurata (1959). Test temperatures: [a.1]6.2–8.9°C, [a.2]8.7–9.4°C, [a.3]11.7–13.9°C. Kurata's original chlorosities converted to salinities; response distributions replotted. Converted salinities for >100% seawater, recalculated here, are lower than those shown in some earlier references to Kurata's data.

[b]Tested at 8.5°C; previous incubation experience, 20‰ at 8.5°C (Alderdice et al. 1979a).

[c]Dueñas (1981). Averaged for test temperatures of 6, 9, 12°C; previous experience: [c.1]21‰, 12°C; [c.2]21‰, 6°C.

Kurata's (1959) estimates (42.1, 41.9, 37.0, 33.5‰) for 2-, 5-, 7-, and 19-d-old larvae (Table 2) approach this condition. On the other hand, salinity resistance may not be constant with increasing larval age, and the 3-d LC50s (Table 2) provide such a comparison for larvae at different ages. One will note that only the 19-d LC50 approaches an estimate of salinity at the incipient lethal boundary. A further source of variability in such estimates, that associated with acclimation, has been demonstrated by Dueñas (1981) to arise from salinity–temperature experience during egg development. In her original data, based on 18 combinations of egg incubation salinity (13, 21, 29‰) and temperature (6, 12°C) and larval test temperature (6, 9, 12°C), incubation salinity and temperature and their interaction affected larval salinity resistance significantly, while test temperature did not. The variation in estimates of resistance associated with incubation experience is characterized in the 3-d LC50 estimates for 3-d-old larvae (35.5, 39.0, 48.2‰, Table 2). Note that the range of resistance values for larvae from Dueñas' six incubation combinations (34.2–51.0‰, Table 1) is nearly as large as the range of the remaining estimates in Table 2. Clearly, to distinguish sources of variance associated with larval resistance one must consider (1) test methodology and its association with salinity level and duration of exposure, (2) age of the larvae, and (3) salinity–temperature conditions imposed during incubation. Since salinity resistance may change with larval age (Holliday 1965), a test interval of meaningful length is needed. The shorter the test period, the higher the LC50 will be and the less it will approximate the incipient lethal level. On the other hand, the longer the test period, the greater will the tendency be for the LC50 estimate to "average" resistance over the test period. In general, the 3-d LC50 would seem a useful compromise, for example, for estimating *relative* salinity resistance as influenced by larval age.

More realistic estimates of salinity-induced mortality near the incipient lethal boundary may be obtained from 3-d LC10 measures, salinities associated with 10% mortality of larvae over a 3-d test period (Table 3). Such estimates are obtainable from the same distributions of response that provide the 3-d LC50 salinities. Although the available data are limited, they indicate that survival of larvae at higher salinities is maximized on a ridge running from low salinity–low temperature to high salinity–high temperature conditions during egg incubation. Eggs incubated at the low/low or high/high combinations (13‰, 6°C; 29‰, 12°C) are more resistant to higher salinities (33.8 and 34.0‰, respectively). In contrast, low/high and high/low combinations (13‰,12°C; 29‰, 6°C) result in lower resistance estimates (22.3 and 31.7‰, respectively). Hence, the salinity–temperature interaction that influenced total hatch and hatch of viable larvae appears to have a similar impact on salinity resistance during early larval stages. Incubation temperatures of 12°C (Table 3) are beyond the range of most spawnings in British Columbia waters and spawning salinities are mostly in the range of 27–28.7‰. Thus, the remaining estimates in Table 3 suggest that upper incipient lethal levels of salinity (3-d LC10, 3-d-old larvae) for Pacific herring larvae are likely to be near the range of 27.5–31.7‰.

TABLE 3. Estimates from the literature of upper salinities (‰) associated with 10% mortality (3-d LC10) for larvae 0–3 d old.

Acclimation (incubation) temperature (°C)	3-d LC10 (‰) for acclimation (incubation) salinity: 13	20	21	29
6	37, 33, 32 (mean 33.8)	—	31, 31, 29 (mean 30.3)	32, 32, 31 (mean 31.7)
8.5	—	27.5[a]	—	—
12	25, 20, 22 (mean 22.3)	—	27, 28, 25 (mean 26.7)	31, 37, 34 (mean 34.0)

[a]From Alderdice et al. (1979a); remaining estimates from Dueñas (1981).

It has been suggested that unfed larvae may show lower resistance to salinities above 20‰ (Holliday 1965). Three-day LC10 estimates for unfed larvae at 8.5°C (Alderdice et al. 1979a, their fig. 8) place resistance levels at 27.5, <20, 33.5, and 23‰ for larvae 3, 6, 9, and 12 d old at completion of the tests. The larvae were from eggs incubated at 20‰, 8.5°C. Unfortunately, lack of data on fed larvae prohibits further comparison. We conclude that the possible influence of feeding on salinity resistance and tolerance of herring larvae also merits further attention.

Fate of Larvae in Offshore Waters

Based on the experimental evidence, what can be inferred about the fate of Pacific herring larvae in offshore waters? Generally, Pacific herring in British Columbia waters do not spawn on unprotected ocean coastlines. They make use of inside waters, the more protected coastlines of inlets and embayments. There, coastal salinities are somewhat lower than oceanic levels. The Strait of Georgia between Vancouver Island and the mainland is typical of these protected waters. In one inshore region of the Strait, Arai and Hay (1982) found densities of Pacific herring larvae (1981, Baynes Sound) in the upper 5 m to range from $1200 \cdot 10\ m^{-3}$ at the time of maximum larval density (30 March), reducing to $150 \cdot 10\ m^{-3}$ on 7 April and $30 \cdot 10\ m^{-3}$ on 14 April. Lacking more general data, these are taken as

estimates of larval density for inshore waters of Georgia Strait during the hatching period. At the same time (1981), a number of ichthyoplankton surveys were conducted to determine the distribution and abundance of fish larvae in offshore, deeper waters of the southern portion of the Strait (Mason et al. 1982a, 1982b). Distribution and abundance of herring larvae in offshore waters are shown (Fig. 2) for four cruises (16–22 March, 30 March–6 April, 14–20 April, 27 April–3 May). Surface salinities and temperatures representative of the area of main offshore abundance (Fig. 1B, ≥ 2 larvae·10 m^{-3}) are shown in Table 4. The first cruise (16–22 March) found very low larval densities in the open waters (Fig. 2a) with a small concentration (0.1–0.4·10 m^{-3}) at the southern end of the Strait. The second cruise (30 March–6 April) sampled larval distribution associated with the major period of inshore hatching (Fig. 2b). The third cruise (14–20 April) shows an extension of distribution northwards and a large reduction in numbers in the earlier region of higher larval density (Fig. 2c). In the fourth cruise (27 April–3 May), offshore larval density again is very low (Fig. 2d). Integrating the areas of larval concentration (Fig. 2) and assuming that larvae are found mainly in the upper 10 m, an indication of larval numbers may be obtained for the offshore waters examined:

Period (1981)	No. of larvae in offshore waters	Relative abundance (larvae·m^{-3})
16–22 Mar.	9.7×10^6	0.04
30 Mar.–6 Apr.	5.1×10^9	24
14–20 Apr.	4.2×10^9	19
27 Apr.–3 May	5.0×10^7	0.23

The rate of disappearance of herring larvae from the offshore waters during the first half of April is about 9% per week. However, in the inshore waters of Baynes Sound during approximately the same period (Arai and Hay 1982) the rate of disappearance of larvae was about 45% per week. A cautious comparison of these estimated rates of reduction would admit the possibility of some relocation of larvae from Baynes Sound into the Strait. Yet, if salinity tolerance were limiting survival of larvae in the surface waters of the Strait (27.3–28.6‰, Table 4) one might expect a more rapid decline in larval density there compared with that for Baynes Sound. Based on the evidence, admittedly incomplete, we suspect that waters of 27.3–28.6‰ have little influence on larval survival in open waters of the southern Strait of Georgia. Further data from the region of main larval abundance (Fig. 2b, 30 March–6 April) support this contention. The larvae obtained by Mason et al. (1982a, 1982b) were preserved immediately in 4% formaldehyde–seawater solution from tows largely of 10–20 min duration. Mean length of fixed larvae was 14.72 mm. Assuming a shrinkage of 18% for larvae from tows > 10 min duration, the original live length of the larvae (mean ± 1 SD), evaluated from Hay (1981, 1982), is 16.24 ± 2.89 mm. The origin of the concentration of larvae centred off Gabriola Island (Fig. 2b) is uncertain. Mean size and wide dispersion of the larvae, known wind-driven surface water circulation patterns in the period considered (Waldichuk 1957), and location, size, and timing of spawnings in the whole region (Hourston and Haist 1981) circumstantially identify Nanoose Bay, northwest of Nanaimo (Fig. 2b), as the most likely source of these larvae. There, a major spawning occurred with maximum egg deposition on 3 March 1981. Assuming that the larvae sampled originated from Nanoose Bay, they would be about 15 d old in the concentration off Gabriola Island at the time of capture. Two of the larvae examined had vestiges of yolk remaining, i.e. about 1% of the larvae were <7 d old. From an estimated 8.5–9.0 mm length at hatching (Alderdice and Velsen 1971) the larvae, assumed from Nanoose Bay, would have grown at a rate of 0.48–0.52 mm·d^{-1} at temperatures of 8.8–9.1°C to achieve the calculated mean length of 16.24 mm. The estimate may be compared with that obtained from the (1974) data of von Westernhagen and Rosenthal (1979, their fig. 1b) for larvae (~ 14 mm) of the same presumed age from the nearby inshore waters of Departure Bay. Growth rate of their larvae was about 0.46 mm·d^{-1} at temperatures of 10.1–11.5°C. In addition, 42% of the larvae taken off Gabriola Island had food in the gut. From Hay's (1981) results for 23- and 10-d-old herring larvae captured in a net, one would expect 57–68% of the Mason et al. (1982a, 1982b) towed larvae to have had food in the gut prior to capture, the difference being attributed to gut evacuation under the stress of capture. Under these circumstances, food supply and growth would not appear to be factors limiting survival. The available evidence suggest that Pacific herring larvae over the first 2 or 3 wk after hatching can tolerate salinities of 27.3–28.6‰ at temperatures of 8.8–9.1°C without difficulty. Although some of the decline in numbers of larvae in the open waters of the Strait of Georgia may be attributed to further dispersal of the larvae, most of the decline would appear more likely to be the result of predation, rather than starvation or lack of tolerance to surface salinities.

There is considerable evidence, albeit mainly qualitative, that predation on Pacific herring larvae in Canadian waters could be extensive. Stevenson (1962) reported an observation of a layer of ctenophores (*Pleurobrachia* spp.) so dense as to show a false bottom on a sounder tracing. The ctenophores were feeding on larval herring as the larval passed through the layer on their diurnal vertical migrations. He also reported predation on larvae by jellyfish (numerous species) and chaetognaths (*Sagitta* sp.). Arai and Hay (1982) estimated that the medusa *Aeqorea victoria* could have consumed 9% per day of the herring larvae in Baynes Sound during the peak of larval abundance in 1981. von Westernhagen and Rosenthal (1976) observed predation by juvenile and adult *Hyperoche medusarum* so intense that concentrations of these amphipods were capable of eliminating large concentrations of herring larvae within a few hours. Nor is predation on larvae limited to zooplankters. Adult herring have been observed feeding voraciously on newly hatched larvae (Hourston and Haegele 1980), and juvenile herring can consume several larvae per minute when they occur concomitantly (Hourston et al. 1981). Young salmon also can be major predators when their seaward migration takes them through concentrations of larvae.

Discussion

Information is sparse on the mechanics of respiration of eggs in an egg mass. We suspect that four factors are involved in oxygen transport and metabolite removal: (1) perivitelline fluid colloid osmotic pressure, (2) natural convection, (3) the surge associated with water movement influenced by wave action, beach slope, and depth, and (4) possible differences in convective flow of deoxygenated water from an egg mass in relation to the posture of the substrate (e.g. horizontal rock or more upright vegetation). Water transport through the egg mass, driven by these four factors, also would be influenced by deposition intensity and packing density of the eggs. A better understanding of these relations would require an estimate of percentage open space, the interstitial volume between eggs, in

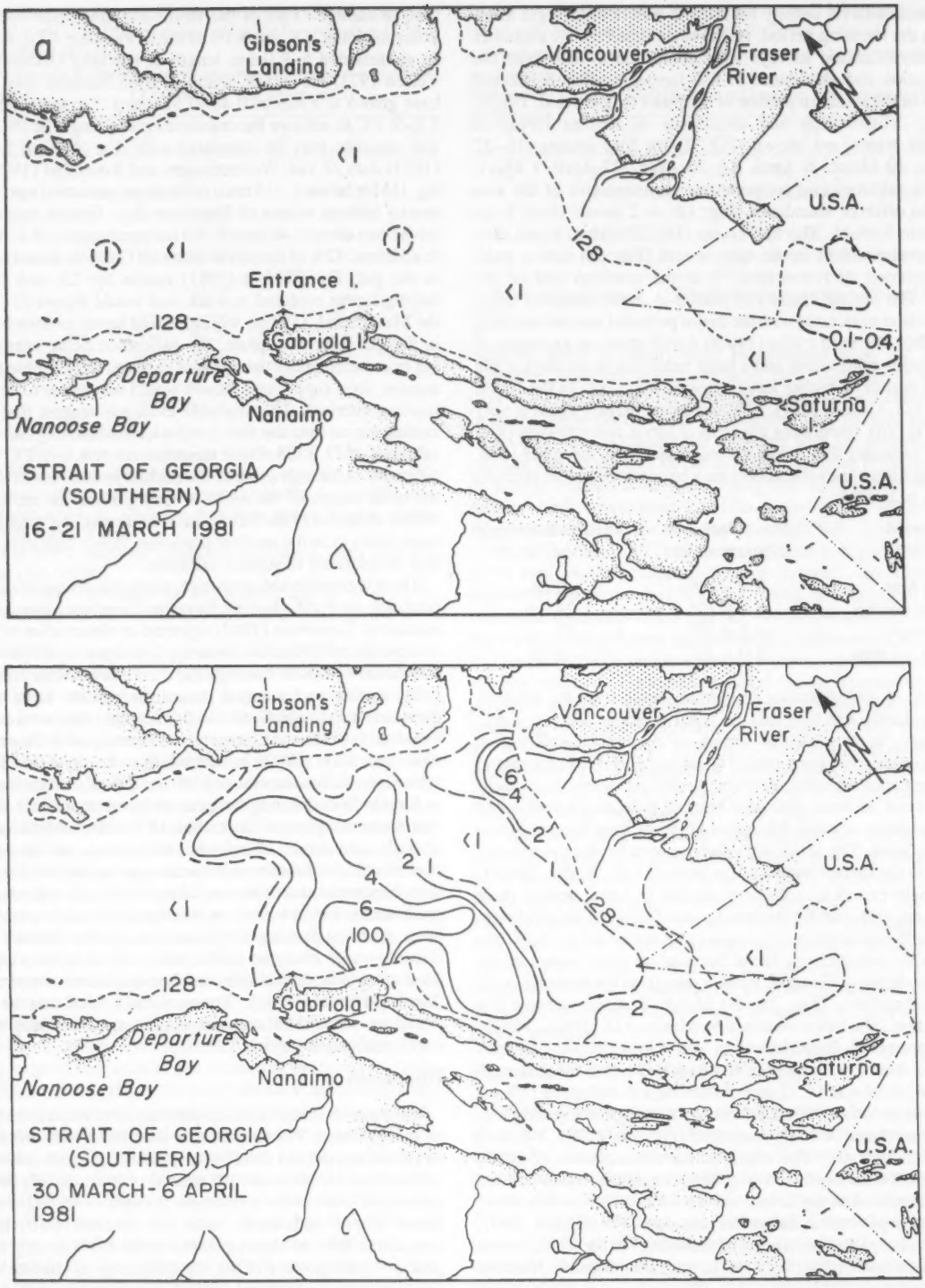

FIG. 2. Distribution of Pacific herring larvae in open waters (broken line is the 128-m depth contour) of the central and southern portion of the Strait of Georgia, B.C., on four ichthyoplankton cruises employing an 80-station grid (a, 16–22 March; b, 30 March–6 April; c, 14–20 April; d, 27 April–3 May) during 1981 (Mason et al. 1982a, 1982b). Distribution of larvae shown as <1, 1, 2, 4, 6, and 100 larvae·10 m^{-3}.

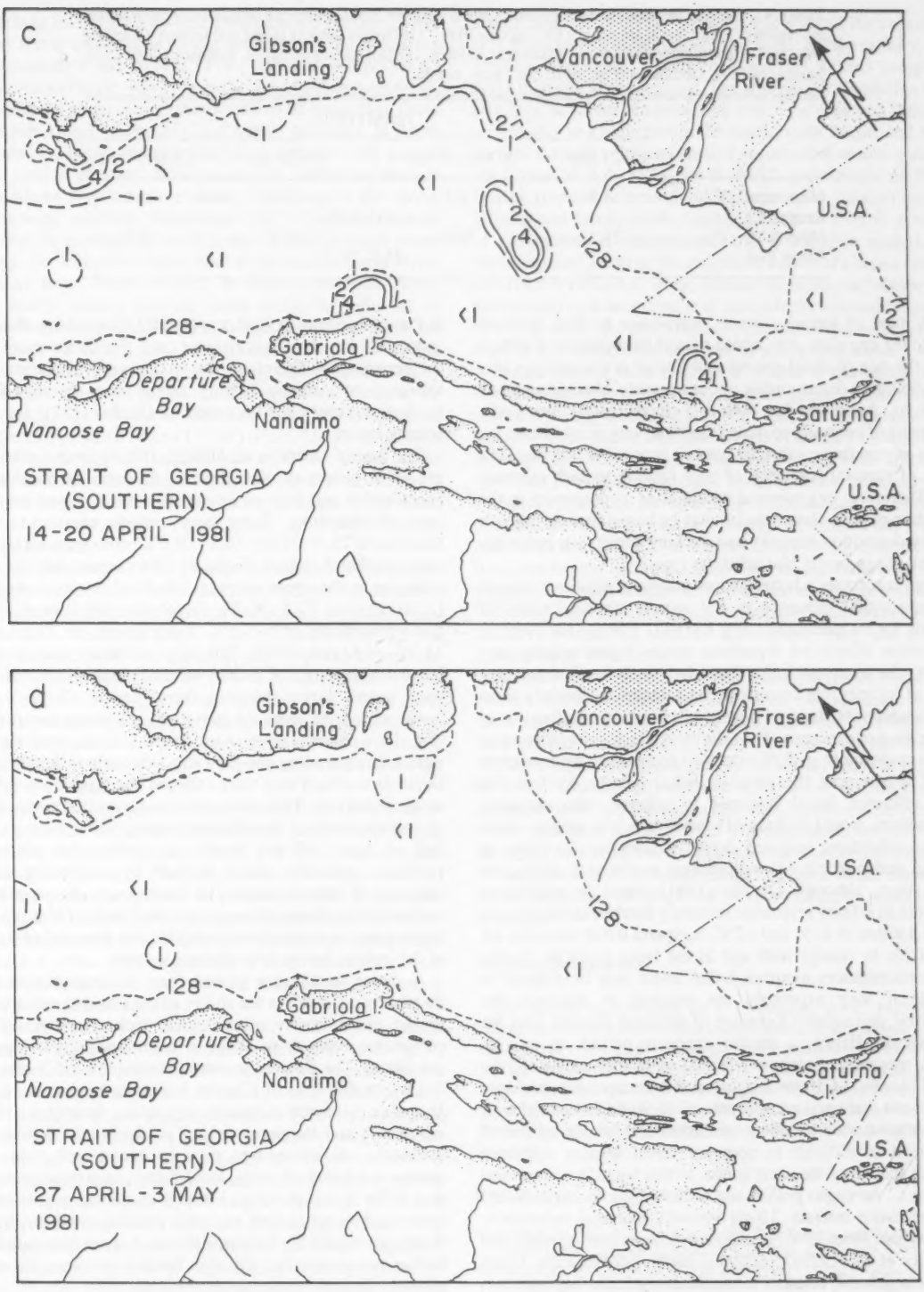

FIG. 2. (*Concluded*)

TABLE 4. Surface salinities and temperatures in the southern Strait of Georgia indicative of those within the region of major larval abundance (≥ 2 larvae$\cdot 10\,m^{-3}$) between Gabriola Island and Gibson's Landing (Fig. 2). Surface temperatures from Mason et al. (1982a, 1982b); surface salinities, Entrance Island Light Station, from A. Dodimead (Pac. Biol. Stn., pers. comm.).

	Period (1981)			
	16–21 Mar.	30 Mar.–6 Apr.	14–20 Apr.	27 Apr.–3 May
Mean temp. (°C)	8.8	9.1	9.7	10.0
Range (°C)		8.2–11.0		
Mean salinity (‰)	27.7	28.6	27.3	28.3
Range (‰)		25.0–29.3		

an egg mass of known volume. Resistance to flow of water through the egg mass also would require examination. Furthermore, the rate of development and fate of occluded eggs in a mass should be determinable under a variety of environmental conditions. Assuming that both deposition intensity and packing density of naturally spawned eggs can vary in relation to the species of vegetative substrate used, it is possible that there is a matrix of survival potentials of eggs relative to each substrate type. Therefore, egg survival potential as a component in the estimation of year-class strength may be better approximated in terms of deposition intensity and packing density, or indirectly in terms of egg layers and substrate type.

In herring larvae, a better understanding of salinity tolerance and factors that influence it will require standardization of methods for its estimation. Fry's (1947) scheme for defining temperature effects on organisms seems highly appropriate. That is, the incipient lethal boundary is defined, separating levels of salinity the organism can tolerate indefinitely from those in which resistance is limited as a function of salinity level and duration of exposure. The salinity at which exposure time to a given response (e.g. 50% survival) approaches an asymptote should approximate the incipient lethal salinity. Factors that could influence larval response to salinity, also requiring examination, would include (1) larval age, (2) salinity–temperature conditions imposed during incubation, (3) effect of feeding, and possibly (4) temperature acclimation during the larval stage, although Dueñas (1981) found no significant difference in salinity resistance for newly hatched larvae (from 6 or 12°C) tested at 6, 9, and 12°C. Incipient lethal salinities are most likely to change with age as the larva develops. Under these circumstances incipient lethal levels may be difficult to estimate if long exposures are required to approach the asymptote, and salinity tolerance of the larva changes over the test interval. Hence, a shorter exposure period, to provide *relative* measures of response, would seem appropriate and the 3-d LC50 or 3-d LC10 are suggested. It is unnecessary, perhaps, to point out that until components of variance associated with the aforementioned variables are understood for one species of *Clupea*, it is difficult to compare larval salinity tolerance between species of the same genus. In this regard a comparison between *C. harengus pallasi* and *C. harengus harengus* would seem of major interest. Using virtually identical techniques, Holliday and Jones (1965), studying Atlantic herring eggs, and Alderdice et al. (1979a), studying Pacific herring eggs, found that ion regulation relative to incubation salinity followed two fundamentally different courses in the two forms. In addition, Atlantic herring larvae appear to tolerate higher salinities than Pacific herring larvae. Osmoregulation in Atlantic herring eggs was found to be substantial; some regulation was found to occur in Pacific herring eggs but, comparatively speaking, the former appear to be an osmoregulator and the latter more of an osmoconformer. Therefore, one wonders to what extent salinity tolerance in Atlantic herring larvae may be modified by incubation experience, as found by Dueñas (1981) for Pacific herring larvae.

The data of Mason et al. (1982a, 1982b) for the offshore but protected waters of the Strait of Georgia demonstrate that considerable numbers of larvae may move out of the littoral zone after hatching. There they would be exposed to surface salinities of 27.3–28.6‰ (8.8–10.0°C) during the hatching and early posthatch period (Table 4). We suspect that the closest estimates to the upper incipient lethal salinity level are the 3-d LC10 values of 27.5–31.7‰ (incubation salinities of 20–29‰ and temperatures of 6–8.5°C, Table 3) and the 19-d LC50 of 33.5‰ of Kurata (1959). The range of these values is close to but above the range of surface salinities in the Strait of Georgia open waters during the early larval period. Of the captured larvae examined from the period of maximum larval density (Fig. 1b) a majority were an estimated 15 d old. As these larvae were actively feeding and growing, we conclude that the surface salinities to which they were exposed had little if any influence on their survival. Therefore, we assume that the estimated rate of disappearance of the offshore herring larvae during the first half of April (9% per week) may reflect the influence of predation, possibly offset in part by continuing seaward dispersal of inshore larvae. In comparison, disappearance of inshore larvae during the same year and period (45% per week) is presumed to result from predation, and dispersal of a portion of the inshore larvae into offshore waters.

A major impression gained from an examination of the literature on *Clupea* is the ability of the genus to accommodate to and use a variety of ecological niches as a result of its euryplastic capacity to adapt to various salinity–temperature conditions. The Soviet literature (Svetovidov 1952) recognizes five major divisions of *Clupea*: *harengus harengus*, *harengus harengus* n. *membras*, *harengus pallasi*, *harengus pallasi* n. *suworowi*, and *harengus pallasi* n. *maris-albi*. Within these divisions, various groups may be recognized, and within groups, a number of races, local forms, or populations. These may differ in morphology, location of spawning grounds, and time of spawning, spring, summer, autumn, or winter. In North American waters *C. harengus pallasi* has not been subdivided further taxonomically, although there is evidence for at least partially discrete spawning populations.

Over the total range of the Pacific herring, numerous reproductive strategies appear to be followed in relation to local conditions. Whether these constitute genetic or environmental adaptations is unclear. Spawning in North American popula-

tions tends to follow a north–south temperature gradient, more northerly forms spawning at similar temperatures but later in the season (Alderdice and Velsen 1971), although exceptions do occur. In Asian Pacific waters from the Sea of Japan northward, spring seasonal water temperatures tend to be lower than those in the North American Pacific Coast part of the range. In Asian Pacific waters, Pacific herring may enter estuaries and ascend the tidal portion of rivers. Some move into semisaline lakes or lagoons where they may overwinter, spawning in the spring before moving seaward (Svetovidov 1952). In Soviet Arctic waters, Pacific herring are found in the vicinity of major rivers including the Indigirka River and as far as the Lena River (Olenekski Bay, Tiksi; 122°E). In North American Arctic waters, Pacific herring also are found within the influence of major rivers. In the Beaufort Sea it had been taken from the Yukon shores of Mackenzie Bay (Kendel et al. 1975) and eastward (Mallik Bay, Eskimo Lakes, Tuktoyaktuk) (Percy 1975). It has been taken in Liverpool Bay, at Cape Bathurst, up the Mackenzie River as far as Aklavik (Hunter 1975) and as far east as the Coppermine River (115°W) (Percy 1975). It has been "reported" as far east as Bathurst Inlet (109°W). In the colder waters of both Asian and North American parts of the range the relation between cold water temperature and less saline water seems to be a dominant characteristic of Pacific herring spawning habitat.

Having examined briefly the basic characteristics of environments associated with Pacific herring distribution, it seems appropriate to question the general importance of salinity and temperature in the reproductive cycle of Pacific herring. One might conclude that the two factors are not of prime importance within the ranges mentioned because of the euryplasticity and broad compensatory ability of the species. Yet, within these ranges the influence of a salinity–temperature interaction (Fig. 1) on the reproductive cycle, and therefore on geographic distribution, may be of central importance. The following argument is offered:

The Pacific herring appears to have an optimum salinity–temperature centre for maximum physiological performance during its early life history in the region of 12–17‰ at temperatures near 6.5–8.3°C. Over a broader reproductive range of about 0–10°C the organism appears to compensate for temperature change through osmoregulatory adjustment to sustain reproductive performance around the optimum within a spawning range of about 2.6–35‰. This physiological range extension would be achieved in environments where reduced temperature is coupled with reduced salinity.

For example, many of the low-salinity habitat adaptations recorded are associated with Asian North Pacific and Arctic, and western Arctic populations where temperatures in the reproductive period are lower in relation to regional oceanographic conditions and higher latitudes. In more temperate locations one would expect climatic extremes to play a smaller role, near the centre of physiological performance, so that associations with lower salinity waters would be less important and less evident in reproductive habitat selection. In British Columbia waters this seems to be true. Spawning grounds often are found near the influence of freshwater, yet the advantages of such locations in relation to reproductive strategies are not obvious. Further inferences apply to the pan-Pacific distribution of the species, from the Yellow Sea and northern Japan around the perimeter of the North Pacific, into the Arctic, and south in the western Pacific to San Diego Bay, California. We suspect that Pacific herring with the same salinity–temperature performance range (2.6–35‰, 0–10°C), but without the capacity to alter reproductive habits under the influence of the salinity–temperature interaction, would show a much altered geographic range than that now occupied. The advantages of utilizing lower salinities at colder temperatures would be removed, resulting presumably in a reduction in the Asian North Pacific and Arctic parts of the range. In summary, it appears that within spawning conditions of 2.6–35‰ and 0–10°C, populations of Pacific herring respond selectively to the interactive relation between salinity and temperature, enabling them to exploit a variety of environmental circumstances as compatible reproductive environments. Perhaps the enigmatic nature of *Clupea* (Blaxter and Hunter 1982) has some foundation in the euryplasticity of the species: such an animal may have a high potential for genetic diversification, and given the environmental options in which to express it, a greater opportunity for active speciation.

Pacific herring have evolved a system of spawning-ground selection and spawning behaviour that appears to maximize the potential for egg and larval survival. This involves spawning on suitable vegetation in sheltered waters. Yet many locations with these qualities have not, in historical record, been utilized by spawning herring! Presumably, such locations lack some other essential ingredient for spawning success such as a suitable temperature–salinity regime or other environmental requirement. The tendency for the centres of spawn deposition to vary from year to year within the spawning range of individual stocks suggests that such requirements are local and dynamic, perhaps involving interrelations between characteristics of the immediate environment, as well as behavioural traits and state of maturation of the adults.

Historically, strategies for the management of herring resources essentially have been based on two variables: tons of catch and units of effort. With time, such methods frequently have proved inadequate as human pressure on the resource increases. Improved management invariably leads to the need for more detailed and specific information on the resource organism itself: its biological capacities, environmental requirements, and their interrelations. The arguments and inferences presented herein lead us to conclude that a better understanding of the reproductive cycle and its egg and larval stages is essential to the continuing development of more effective management strategies.

Acknowledgments

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Year-Class Strength and Survival of O-Group Clupeoids[1]

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Smith, P. E. 1985. Year-class strength and survival of O-group clupeoids. Can. J. Fish. Aquat. Sci. 42 (Suppl. 1): 69–82.

Global marine fish catch has been stable over the past decade but the clupeoid contribution has declined from one-half to one-third of the marine fish catch. This decline appears to be caused by changes in recruitment success during heavy fishing pressure. Theoretical population approaches and correlative environmental indices are not yet sufficient for setting catch limits. For some time the direct measurement of current biomass appears to be necessary for setting clupeoid quotas. Precision and cost studies on the estimation of biomass with current methods indicate that a standard error of estimate less than 25% cannot be justified based on the increased long-term yield of the stock. Assembly of a prospective life-table for the central subpopulation of the northern anchovy (*Engraulis mordax*) allows the discussion of intra-population and environmental controls on growth of the population. Using reasonable values for survival and growth in the embryonic, larval, and juvenile stages in the context of a life-table allows one to evaluate the stages where recruitment is controlled. From this manipulation it appears that significant decreases in recruitment could originate at any stage but marked increases in recruitment are only likely to arise from lower mortality rates in the embryonic and larval stages. The late larval stage of the anchovy could exhibit remarkable control on the level of recruitment through plasticity of the interaction between growth rate and survival. Maximum cohort biomass of the anchovy occurs late in the first year of life but current measures of juvenile survival and biological production are inadequate to explore density-dependent survival and growth rates.

La prise globale de poissons marins a été stable au cours de la dernière décennie mais le pourcentage de clupéidés est passé de la moitié au tiers de ce total. Ce déclin semble être causé par des variations du succès du recrutement quand la pression par pêche est élevée. Les modèles théoriques de population et les indices environnementaux corrélatifs ne permettent pas encore de fixer les limites des prises. Pour quelque temps, la quantification directe de la biomasse actuelle semble nécessaire pour l'établissement des contingents de clupéidés. Des études sur la précision et les coûts des estimations de la biomasse, à l'aide des méthodes actuelles, indiquent qu'on ne peut justifier un écart-type de l'estimation inférieur à 25% en fonction du rendement accru du stock à long terme. L'ébauche d'une table de survie éventuelle pour la sous-population d'anchois du Pacifique (*Engraulis mordax*) permet une discussion des contrôles environnementaux et intra-population sur la croissance de la population. En utilisant des valeurs raisonnables concernant la survie et la croissance chez les stades embryonnaires, larvaires et juvéniles, dans le contexte d'une table de survie, on peut évaluer les stades où le recrutement est contrôlé. D'après cette manipulation, il semble que les baisses importantes du recrutement peuvent se produire à n'importe quel stade, mais que les accroissements marqués du recrutement ne proviendront probablement que de faibles taux de mortalité aux stades embryonnaires et larvaires. À cause de la plasticité de l'interaction entre le taux de croissance et la survie, le stade larvaire avancé de l'anchois pourrait exercer un contrôle frappant sur le niveau de recrutement. La biomasse maximale de la cohorte chez l'anchois a lieu vers la fin de la première année de vie. Toutefois, les quantifications actuelles de la survie des juvéniles et de la production biologique ne permettent pas d'étudier la survie reliée à la densité ni les taux de croissance.

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Marine fish catch has been stable over the past decade at 45 million tons per annum but the clupeoid contribution has declined from one-half to one-third the marine fish catch (Anonymous 1981a). This has occurred through a chronic decline of herring catch and a drastic decline of the anchovy catches partly moderated by a recovery of sardine fisheries (Anonymous 1981a). In 1980, clupeoids represented 80% of the meal and oil fishery products, about 15% of the canned and cured fish, and 7% of the fresh or frozen fish (Anonymous 1981b). The major genera in the commercial fishery are the pilchard or sardine (*Sardinops* spp. and *Sardina pilchardus*, 7 million metric tons (t)), the anchovy (*Engraulis* spp., 3 million t), the oil sardine (*Sardinella* spp., 2 million t), and the herring, menhaden, sprats, and thread herring (*Clupea* spp., *Brevoortia* spp., *Sprattus* spp., *Opisthonema* spp., at 1 million t per genus per year). Fisheries are conducted on all ages and sizes of the clupeoids, and variations in recruitment have immediate effects on the fishery. In the past 30 yr the anchovy catch has ranged between one half and 15 million

[1]This paper was presented at the International Symposium on the Biological Characteristics of Herring and Their Implication for Management, convened at Nanaimo, B.C., June 20–22, 1983, commemorating the 75th anniversary of the Pacific Biological Station.

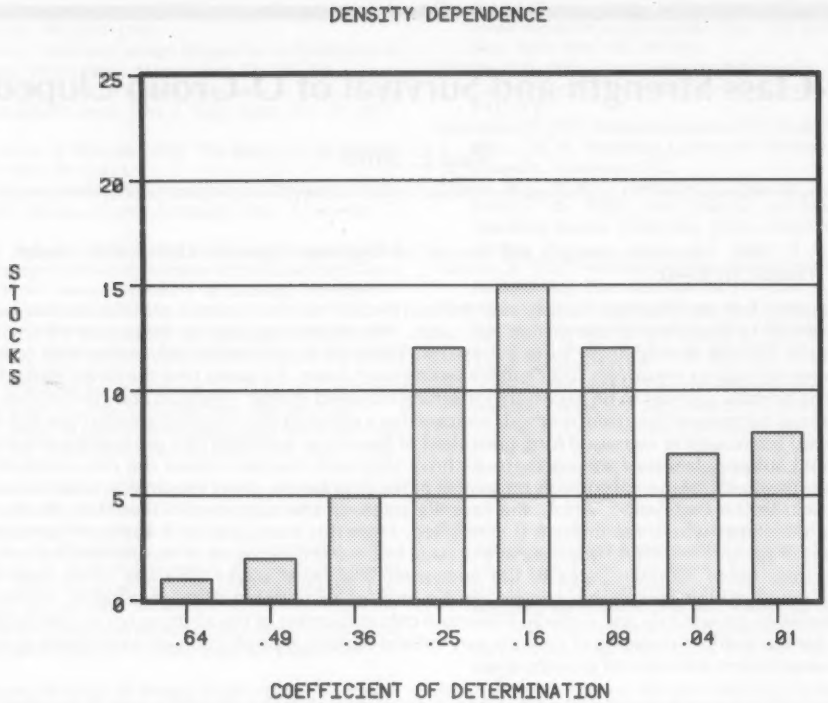

FIG. 1. Frequency distribution of indices of density dependence based on Tanner (1966). The coefficient of determination is the square of the correlation coefficient of the population growth rate versus the population size. All 62 values differ significantly from unity.

$t \cdot yr^{-1}$, sardine has varied between 1 and 7 million $t \cdot yr^{-1}$, and herring from 1 to 5 million $t \cdot yr^{-1}$. Most of this variation has been caused by changes in recruitment success during heavy fishing pressure.

Ten years have passed since Parrish (1973) stated at the Aarhus Symposium on Fish Stocks and Recruitment "... in most species for which detailed information is available, these (population regulation) factors operate mainly during the early stages of development (i.e. between the egg and the end of the first year of life) so that year-class strength is determined and population control mechanisms for most fish stocks operate before the individuals enter the exploited phase."

Improvement of the long-term management of clupeoids stocks will include (1) specialized studies on population size and environmental controls of reproductive success and (2) implementation of measurement and prediction procedures for controlling the impact of fishing pressure on clupeoid stocks.

The theory and application of population modeling does not appear to have much immediate promise for management of clupeoid stocks. A good example of the inadequacy of "density-dependent" controls on population growth is reported by Tanner (1966). Figure 1 is a summary of 111 time series of the relative amount of population change controlled by population size. In the 62 population time series where density and population growth were significantly negatively correlated, the degree of control was very low. Essentially, only 16% of the population growth was controlled by population size. More recently, MacCall (1980a) deduced that as little as 10% of the variation in mortality rate in the northern anchovy (*Engraulis mordax*) could be attributed to density-dependent causes.

Garrod and Colebrook (1978) have presented a large correlation matrix for 22 yr (1950–71) of recruitment of 18 North Atlantic stocks. If large-scale environmental features were a dominant influence on recruitment, independent of stock size and density, one would expect three modes: a positive mode would arise from stock pairs whose recruitment is favored by the same environmental features (i.e. positively correlated recruitment), a negative mode would arise from pairs of stocks in which an environmental change would simultaneously increase the recruitment of one stock and decrease recruitment of the other, and a central mode would arise from indifference of stock pairs' recruitment to general environment.

Figure 2 is a frequency diagram of the 153 stock pairs coefficient of determination (r^2). Coefficients of determination arising from negative correlations are separated from those arising from positive correlations. If one assumes no serial coherence with this length of time series, P = values of r^2 in excess of 0.25 ($0.05 < t < 0.01$) is strong evidence of association in the statistical sense that such a value would not likely arise by chance; however, a coefficient of determination as low as 0.25 on the interannual scale would have very little use in fisheries management or biological oceanography. More than two thirds of the pairs were positively correlated. This implies that certain general features of the environment such as lethal temperatures, turbulent mixing, and productivity have a weak large-scale, long-term control on population success, irrespective of population reproductive size.

General population theory and wide-scale environmental measurements may never provide adequate (Fig. 1 and 2) information for generating periodic decisions necessary to restore

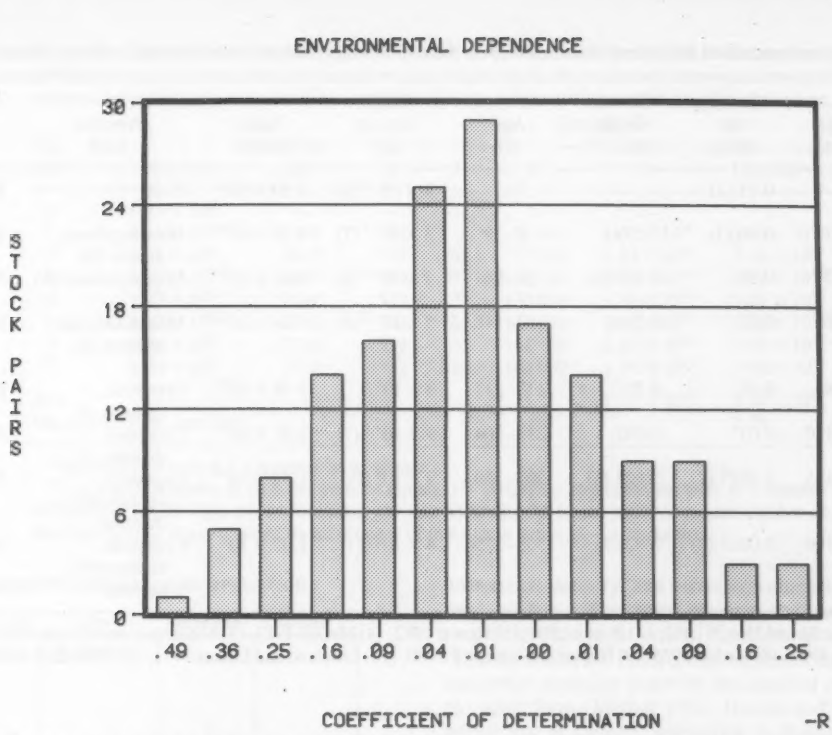

FIG. 2. An index of environmental dependence based on Garrod and Colebrook (1978). The coefficient of determination is the square of the correlation coefficient of all pairs of 18 North Atlantic stocks.

and sustain clupeoid fisheries. Until predictions of recruitment success are effective, management of clupeoids will depend on assessments of stock size and direct measures of recruitment. Gulland (1982) stated that "... the point in their lifespan (fishes) in which increased understanding would seem to be most rewarding is in the early life stages before recruitment ... The practical value of such an improvement in our scientific knowledge in terms of better management of the world's fish resources is considerable." It is the purpose of this paper to explore characteristics of the early life stages of the northern anchovy and the practical value of new procedures for restoration and management of clupeoid fish stocks.

Mechanisms of Population Control

The habitats of clupeoids are not known in sufficient detail to decide for any species what mechanisms other than fishing control reproductive success, population size, and potential fishery yield. The sheer logistics of mounting population/habitat studies with sufficient geographic scale, spatial intensity, and temporal continuity and competent samplers have so far prevented adequate explanations of annual fluctuations of clupeoid reproductive success. For convenience, most work on the stock-recruitment problem has had to accompany stock assessment activities. Similarly, most analytical work has been concentrated on the commercial sizes and planktonic stages. The result is that time series data are too simple and the occasional experimental approaches are too short-term to provide adequate information on the basis of recruitment overfishing in clupeoids.

I shall defer to the second section how early and how precise a recruitment prediction must be to be worth the cost of producing the estimate. For the purpose of this section I will assume that timely knowledge of recruitment success will be valuable for effective tactical management of clupeoids and some knowledge of recruitment variability will encourage strategic approaches to the limitation of overall fishing effort and associated capital facilities.

This section contains a prospective life-table of the northern anchovy central subpopulation. This is intended to focus the discussion in the subsequent elements of this section on where the life-cycle and in what manner the density-dependent and environmental mechanisms serve to control population size in *E. mordax*. The second element is a description of some density-dependent mechanisms. Lastly, environmental mechanisms are discussed.

General Features of an Anchovy Population

Vulnerability to predation and starvation changes so radically during the life cycle of a clupeoid that it is useful to erect a life-table as a guide to stages in which population size control by intrapopulation or environmental means may be effected. It is the purpose of this section on the population characteristics of the central subpopulation of the northern anchovy to describe the entire life cycle. While we have detailed knowledge of only the adult and planktonic stages (Smith and Lasker 1978), we can deduce the intermediate parameters for a first approximation. This is accomplished by the artifice of a stationary population model. New estimates of fecundity and growth (Hunter and Leong 1981; Mallicoate and Parrish 1981) for this subpopulation can be used with estimates of embryonic mortality (Picquelle and Hewitt 1983) and larval growth (Methot and

TABLE 1. Estimated and postulated life history characteristics for the central subpopulation of the northern anchovy (sources in parentheses).[a]

Category	Length (mm)	Mortality rate (daily)	Growth weight ($mm \cdot d^{-1}$)	Age (d)	Initial dry wt (g)	Initial number	Principal food	Principal predators
Embryo	Egg–4	0.25 (1)	—	0–7	3×10^{-5} (6)	3.50×10^{15}	Yolk	Filtering, biting (9, 10, 11, 12)
Early larva	4–10	0.16 (3)	0.5 (4)	8–19	2×10^{-5} (7)	4.74×10^{14}	Dinoflagellates, nauplii (8)	Biting
Late larva	10–35	0.05	0.325 (4)	20–96	5×10^{-4} (6)	6.94×10^{13}	Microcrustacea (6)	Fish, birds
Early juvenile	35–60	0.02	0.5 (4)	97–146	5×10^{-2} (6)	1.48×10^{12}	Microcrustacea, diatoms (4)	Fish, birds, marine mammals
Late juvenile	60–85	0.01	0.35	147–217	3×10^{-1}	5.44×10^{11}	Copepods, diatoms (4)	Fish, birds, marine mammals
Prerecruit	85–110	0.01	0.087	218–504	9×10^{-1} (7)	2.67×10^{11}	Copepods, diatoms (4)	Fish, birds, marine mammals
Early adult	110–135	0.0027 (2)	0.025 (5)	505–1504	2×10^{0} (7)	1.52×10^{10}	Copepods, euphausiids, diatoms	Fish, birds, marine mammals
Late adult	135–160	0.0027 (2)	0.02 (5)	1505–2754	4×10^{0} (7)	1.02×10^{9}	Copepods, euphausiids, diatoms	Fish, birds, marine mammals

[a]Sources: (1) Picquelle and Hewitt 1983, (2) Hanan 1980, (3) Hewitt 1982, (4) Methot 1981, (5) Mallicoate and Parrish 1981, (6) Hunter 1976, (7) Hunter and Leong 1981, (8) Lasker 1975, (9) Hunter and Kimbrell 1980, (10) Lillelund and Lasker 1971, (11) MacCall 1980b, (12) Theilacker and Lasker 1974.

Kramer 1979; Methot 1981) to postulate a total life cycle stationary model.

In Table 1 I have listed the assumed characteristics of the anchovy population. Citations for the properties for which we have any data are listed. These parameters or their range are known only for time periods we have been fortunate enough to observe. The primary utility of listing the known and assumed values is to direct the discussion below to a small number of specific characteristics of the population, and to speculate how these might be influenced by the population size and the environment within the first year.

For all but two of the stages, the population is divided into 25-mm length groups. The first two stages, the embryonic and early larval, are divided from each other on the basis of the onset of feeding: the transition to late larva is arbitrarily set at a length of 10 mm.

The fecundity schedule from which the initial number in Table 1 is derived is found in Table 2. In this instance the fecundity rate is controlled only by the number of batches of eggs per year and the number of eggs per batch at a fixed rate per adult gonad-free weight. I have assumed no weight- or age-specific change in the eggs produced per gram of female. We have no estimate of the variability of the number of batches per year but the batch fecundity appears to vary on the order of 20% on an interannual basis (Hewitt 1982). I also do not know whether the season of slower spawning is based on many females spawning at a slow rate or a few females spawning at the normal rate.

A schematic drawing of a cohort of northern anchovy is illustrated in Fig. 3. The mortality and biomass curves are distorted by the log–log plot of numbers and biomass on age in order to emphasize the role of the early stages. The biomass of the cohort undergoes four transitions, which may be instructional for the study of recruitment. Three of the changes occur in the larval stage and one in the juvenile stage. For the purpose of this discussion, I will first point out some functional anatomical features for each stage and follow with a simple model of their mortality and growth.

Embryo

The embryonic stage is characterized by rapid loss in weight per individual and rapid decline in numbers. As a relatively large member of the zooplankton, the egg is subject to passive filtration. It is also probably vulnerable to biting as the visual distortion of the clear egg, the increasing visual contrast, and later motions of the developing embryo heighten the detectability by mechanoreceptors and vision. The vulnerability may also be heightened at hatching as the protective integument of the egg is lost: clues for chemoreception by predators may also increase. Lillelund and Lasker (1971) described the mortality associated with chance contact of yolk-sac larvae with copepods even when no feeding by the copepods occurs. Theilacker and Lasker (1974) evaluated the predation by euphausiids on yolk-sac larvae. Also, there appear to be many malformed embryos in nature (E. Sandnop, Southwest Fisheries Center, pers. comm.; H. Santander, Instituto del Mar del Peru, Collao, Peru, pers. comm.; E. Stevens, Southwest Fisheries Center, pers. comm.) at all stages; some may live through the yolk-sac period but are too distorted for successful first feeding. The anchovy requires high food density at first feeding; layers (Lasker 1975) and horizontal patches of food (Vlymen 1977) are a condition for successful first feeding. The embryos are never very far from low lethal temperatures (Brewer 1976) in the water column (12°C at 50 m depth; Eber 1977). The adults appear to skirt lethally cold patches of newly upwelled water (Lasker et al. 1981), and embryonic mortality could be caused by lateral advection into those areas. Lastly, chronic and widespread colder-than-average water temperatures would retard develop-

TABLE 2. Life and fecundity table for the females of the central subpopulation of the northern anchovy.

Age (yr)	Number	Weight (g)[a]	Fecundity[b]				
			b	*f*	*n*	*N*	Cumulative
0	1.74×10^{15}	—	—	—	—	—	—
1	2.11×10^{10}	12.8	532	7	24 000	5.00×10^{14}	5.00×10^{14}
2	7.88×10^{9}	16.5	532	20	77 000	6.92×10^{14}	1.38×10^{15}
3	2.90×10^{9}	20.7	532	20	110 000	3.19×10^{14}	9.58×10^{15}
4	1.07×10^{9}	24.4	532	20	130 000	1.39×10^{14}	5.56×10^{15}
5	3.92×10^{8}	27.8	532	20	148 000	5.80×10^{13}	2.90×10^{15}
6	1.44×10^{8}	31.5	532	20	168 000	2.41×10^{13}	1.45×10^{15}
7	8.24×10^{7}	35.5	532	20	189 000	1.56×10^{13}	1.09×10^{15}
Sum						1.75×10^{15}	3.94×10^{15}
Mean generation time (yr)							2.25

[a]Grams wet weight for a representative female.

[b]*b* = batch fecundity in eggs per gram of female; *f* = frequency of batches per year; *n* = number of fertilized female eggs per female adult per year assuming 50:50 sex ratio; *N* = total number of fertilized female eggs spawned by all females of that age in a year; — = immature.

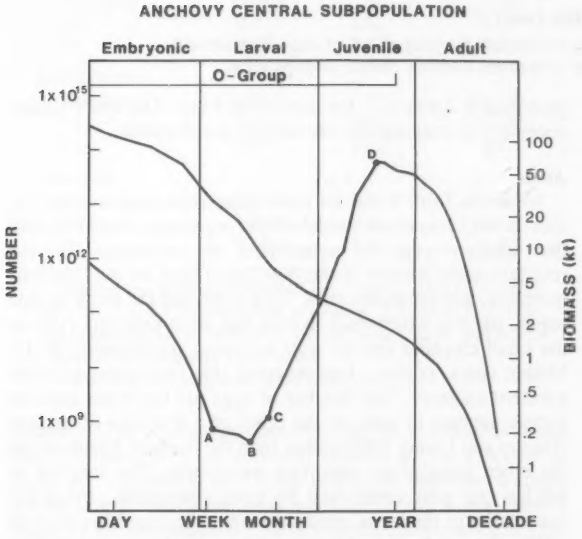

Fig. 3. Cohort estimates of number and biomass of northern anchovy central subpopulation. Values are based on a series of exponential mortality equations for each stage of the life cycle in approximate stationarity.

ment and prolong the highest mortality rate phase of the life cycle.

Larval period

In the larval period, the cohort biomass rate of decline is arrested at point A (Fig. 3) but the growth in weight of the individual larva is insufficient to balance weight loss of the cohort through mortality. At point B the cohort begins its net growth and this growth advances to a sustained high rate at point C. The break at point A may represent a radical change in vulnerability to filtration predation. At this length (5 mm) we see the first demonstrable change in day and night sampling with a 1-m net. Day–night differences in evasion are about 3:1 at this length (Smith 1981). O'Connell (1981) and Hunter and Coyne (1982) have described the onset of schooling and associated anatomical, sensory, and behavioral characteristics. By point B the larva has eye retractor muscles, red muscle and red blood corpuscles, and night vision. Plankton net capture of this stage (15 mm) is a rarity. Point C may represent the faster weight gain and lower mortality aided by the onset of metamorphosis into the adult form (Methot 1981; Hunter and Coyne 1982). The lateral line is formed, respiration is through gills rather than cutaneous, red muscles are in layers, the stomach is formed, and the degree of tolerance to starvation is greatly increased. Sustained high growth rate probably still requires the detection of highly aggregated food supplies (Lasker and Zweifel 1978; Vlymen 1977; Owen 1981).

Juvenile

The maximum biomass of the cohort is achieved at point D in Fig. 3. Methot (1981) pointed out that the elaboration of gill rakers in the juvenile may coincide with the maximum rate of coastal upwelling and diatom abundance (Tont 1981). Methot (1981) also briefly described the concentration of juveniles in the continental borderland. Since the juvenile stage is at a maximum point of biomass and appears to be concentrated in a small fraction of the adult habitat, this would appear to be an extremely vulnerable point for the recruitment to the population by either density or environmentally mediated controls on population growth.

In this simple model, the life cycle is controlled by three factors in each stage. The first factor is the initial number that originates from the previous stage. The second factor is duration or the reciprocal of daily growth rate. The third factor is instantaneous mortality. In Fig. 4, these three factors are illustrated. The contrast of the mortality rate and duration of the early stages may be emphasized by comparison with the nearly horizontal curve of adult mortality. Since these curves are based on stationarity, any combination of increased stage-specific mortality that intersects the adult line will lead to a recruitment below the replacement value. To evaluate the importance of these parameters, it will be convenient to perturb each parameter for each stage.

Mortality

In Table 3, the parameters controlling the hypothetical O-group of the northern anchovy have each been perturbed

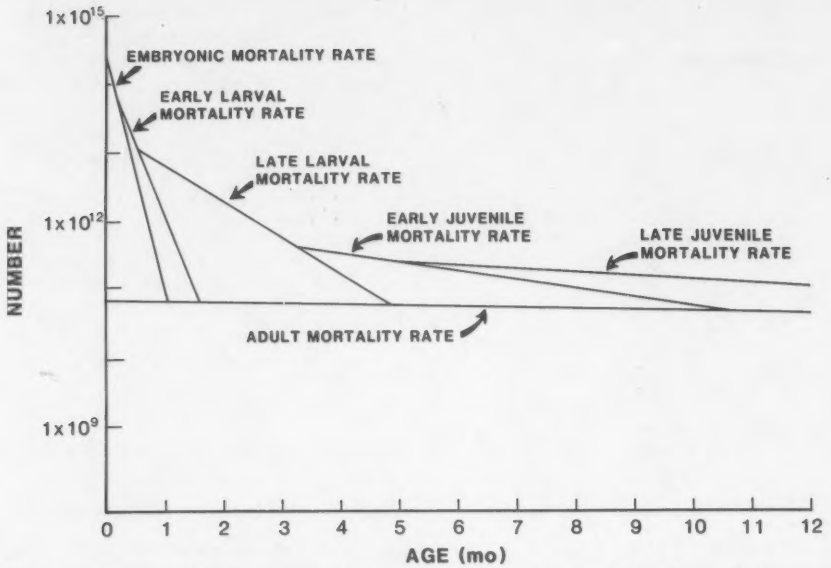

FIG. 4. A diagram of the O-group mortality curves to compare the joint effects of stage duration and stage mortality rate on the resulting adult population of northern anchovy central subpopulation.

sufficiently to effect a fivefold decrease or increase in the level of recruitment. It should be remembered at this point that we do not know if the values we have estimated for parameters so far are central in an interannual sense. The early larval mortality parameter is probably the best known on an interannual scale. The value 0.16 is the mean of 21 annual values in the period between 1951 and 1979. The range is 0.03 and 0.24, and Hewitt (1982) found that the higher values of mortality are associated with higher rates of larval production and wider distribution of the spawn. Interannual variability in embryonic mortality for the brief period between 1979 and 1983 has also been large, with estimated rates ranging from 0.00 and 0.41 in five estimates.

It is interesting to note that no manipulation of the juvenile mortality rates over a period encompassing 4 mo and 50 mm growth in length will result in a fivefold increase in the number of recruits. All the other values for mortality appear reasonable.

Duration

When one deals with duration of the stage or growth rate, it is also seen that a fivefold increase in recruitment cannot solely originate in modification of the juvenile periods' values. At the embryonic stage, the duration is controlled by temperature alone and the parameter requiring that this stage be completed in 1.6 d is not reasonable; thus, a fivefold increase in recruitment does not appear to be a reasonable outcome in this stage alone. The temperature required to lengthen this stage to 14.5 d is nearly lethal as well (Zweifel and Lasker 1976). The observed variations in growth rate in recent years would not support the idea of plasticity to the necessary extent to change the recruitment fivefold (Methot 1981), and field-measured durations of this stage are not distinguishable from the same value measured in laboratory conditions. The late larvae parameter values are as reasonable at both extremes of duration as they are in mortality.

The juvenile and prerecruit duration parameters still retain sufficient plasticity to permit fivefold decreases in recruitment but the only source of a fivefold increase would be the sustained growth at $0.2\ mm \cdot d^{-1}$ for more than 4 mo. The observations necessary to evaluate this are not yet documented.

Adult

We see in Table 2 that the mean generation time is over 2 yr; thus, a fully functional model of this population would require that adjacent years of recruitment be assembled into the resultant adult portion of the population with its own growth, mortality, and fecundity rates. This is beyond the scope of this paper, but it is worthwhile to note that adult mortality rates of the small clupeoid species may well vary significantly. R. D. Methot (pers. comm.) has observed this phenomenon in the northern anchovy. The number of eggs per batch per gram of female appears to vary on the order of a few tens of percent (Hunter and Leong 1981) rather than the fivefold discussed for the other population-controlling parameters. The number of batches per year could well be quite changeable. From the seasonality of the larval production over the past 30 yr (Hewitt 1982), the northern anchovy would not likely vary more than two- or three-fold in the annual rate of fecundity. More directed study on seasonality of adult reproductive behavior is required.

Some Density-Dependent Mechanisms

Some unusual circumstances of density dependence in the northern anchovy are caused by the fact that all but 30 d of a 5-yr life cycle is spent in schools (Hewitt 1981; Hunter and Coyne 1982) and the schools are often found aggregated into school groups (Fiedler 1977). This means that the more obvious forms of competition for food and space appear to be compromised by aggregation behavior. The following section contains comments on competition, cannibalism, and the stimulation of aggregation and growth of predator populations.

Competition

The dimensions of anchovy schools are of the order of tens to hundreds of metres, with most schools in the lower range, and possibly half of the fish are in the few schools more than 90 m in

TABLE 3. Parameter[a] changes leading to a fivefold decrease or increase in recruitment for the central subpopulation of the northern anchovy. Experimental values underlined (see Table 1 for references).

Stage	Instantaneous mortality (daily)	Stage duration (d)	Growth rate ($mm \cdot d^{-1}$)
Embryo			
Stationary	0.250	8	—
1/5	0.454	14.5	—
5×	0.048	1.6[b]	—
Early larva			
Stationary	0.160	12	0.500
1/5	0.297	22.2	0.270
5×	0.026	1.9[b]	3.158[b]
Late larva			
Stationary	0.050	77	0.325
1/5	0.072	110	0.227
5×	0.029	44.5	0.559
Early juvenile			
Stationary	0.020	50	0.500
1/5	0.053	131	0.190
5×	Inf.[b]	Inf.[b]	Inf.[b]
Late juvenile			
Stationary	0.010	71	0.350
1/5	0.033	232	0.108
5×	Inf.[b]	Inf.[b]	Inf.[b]
Prerecruit			
Stationary	0.010	287	0.087
1/5	0.016	449	0.056
5×	0.0044	126	0.200

[a]Parameters in the equation $NT(I-1)\exp[-Z(I)T(I)]$ where $NT(I-1)$ is the number at the beginning of interval I, Z is the instantaneous rate of mortality, T is the time in days, and $NT(0)$ is the annual fecundity (both sexes).

[b]Unreasonable values or Inf. (infinity).

diameter. The maximum observed size of a school is about 400 m (Mais 1974). A common density within a school is $15\,kg \cdot m^{-2}$ (Hewitt et al. 1976). When one considers a single school (Smith 1978) the food available in the water column would be the accumulated excess of production over consumption for the interval since the last school occupied that area. Anchovy schools at any instant occupy less than 1% of their habitat (Smith 1981) but the chances of reencountering an area or encountering an area already fed upon by another school is relatively high for time periods of weeks. All these events together might cause the schools or school groups to move apart where production of food was inadequate, whereas schools might congregate in areas where food production exceeds consumption. At some population size for anchovy, or at some joint biomass of all the plankton-feeding members of a coastal pelagic guild, competition could occur between schools or among school groups.

Competition could occur between adults and juveniles if the adults deploy over a wide area for feeding when productivity is high and reassemble on the brood habitat with the juveniles at the approach of spawning time. By that time, the juveniles are nearly a year old and their food requirements are the same as the adults. The juveniles will have invested most of their energy intake into growth in length and will have relatively less fat than the adults. The outcome, limiting to the population growth rate, might be to delay the onset of spawning by the O-group and lessen the number or repetitive batches spawned by adults.

There is evidence that all or most juveniles go through a coastal phase (Methot 1981) in water less than 90 m (50 fathoms) deep. In the major brood area for the northern anchovy the mainland coast contains 17% and the coastal islands contain 7% of the 25 000 km^2 brood area. Based on capture rate the shallow waters contained at least 70% of the juveniles. Thus, while a habitat calculation based on Fig. 3 might show food to be sufficient, intraspecific food-limited growth could be a factor for juveniles at large population sizes.

Competition is not likely to be a factor in the early larvae of northern anchovy. Growth rates in the sea are similar to those in the laboratory under rich feeding conditions (Methot 1981).

In summary, competition for food is not likely to be a consideration for early larvae. Competition for food should be considered for late larvae (Cushing 1983).

Competition, if any, for juveniles in a cohort may be exaggerated if most of the juveniles must pass through a small, shallow coastal segment of their habitat. Competition between the adult and juvenile segments of the population could be intense at the winter zooplankton and phytoplankton minimum when the adults assemble on the brood grounds at spawning time. Lastly, competition among adults is likely to be between schools that occupy their local habitat intensely and may reoccupy it frequently.

Cannibalism

Cannibalism is a potential density-dependent, population-limiting mechanism for the northern anchovy. Depending on the population size, cannibalism could be important as incidental to filter feeding, it could be accentuated by directed filtering on high egg concentrations, or by switching from biting to filtering behavior.

If schools must perpetually move to support their high food requirement, the population cannibalism would merely entail a school encountering the patch of eggs deposited by it or another school. From the distribution of fish schools I would expect the reencounter of a patch of eggs by the school that spawned it to be a constant probability at all population sizes or a decreasing probability with increased population size. The encounter and incidental filtration of embryos by a different school (than that which spawned it) would be an increasing function of population size.

Eggs of anchovy disperse after being spawned. Hunter and Dorr (1982) found that filtering anchovy would filter selectively in anchovy egg concentrations of $1 \cdot L^{-1}$ or more. This raises the possibility that rather than incidental cannibalism, at certain population levels directed filtration could represent an important shift in the impact of egg cannibalism on the population growth rate.

A third density-dependent mechanism would be switching from biting to filtering at high population sizes. If the preferred food at low anchovy population sizes were herbivorous crustaceans obtained by biting, the probability of egg cannibalism would be low. If the population size actually decreased the population sizes of herbivores, the additional phytoplankton production and the shortage of crustaceans could increase the incidence of filtering to the extent that population growth rate would be controlled.

Brief observations of cannibalism in the northern and Peruvian anchovy (Hunter and Kimbrell 1980; MacCall 1980b;

Santander et al. 1983) indicate that under current population sizes (very low for both stocks), cannibalism is responsible for a relatively small fraction of the mortality of the spawn. If cannibalism becomes an important regulator of the population growth rate it could occur by (1) directed filtering on dense aggregations of eggs, (2) encounter of other schools' patches of eggs, and (3) the anchovy population switching from biting to filtering feeding behavior.

Aggregation and growth of predator populations

The rapid development, mortality, and dispersal of embryos and larvae of the anchovy would make less likely the aggregation and growth of populations that prey on these stages. There is evidence for reproductive success of coastal birds changing in response to juvenile anchovies. It seems likely that populations of marine mammals and fishes could respond to adult anchovies as well. Anderson et al. (1982) described the improved rates of survival of young of the endangered brown pelican population. Should that success continue, the pelican could in turn begin to exercise control of the juvenile survival rate, particularly if most juveniles must pass through the nearshore region, as postulated by Methot (1981).

Scale deposition rates (Soutar and Isaacs 1974) of the major temperate fish stocks were collectively 3 to 5 times greater at the turn of the century (Smith 1978). This coincides with a population minimum of the northern fur seal harvest in 1911, which has been accompanied by a resurgence of the fur seal population and a concomitant decrease in the scale deposition rate (Anonymous 1977, p. 242). The current fur seal population consumes about 1 million t of pelagic fish per year in the Northeast Pacific (Lander and Kajimura 1982). If the high populations of the early part of this century stimulated the growth of the predatory populations this could be an important form of density-dependent control of the anchovy population.

Some recent years of poor recruitment per spawner in the northern anchovy have also been years of unusual Pacific mackerel (*Scomber japonicus*) abundance on the brood grounds (R. D. Methot, pers. comm.). To the degree that the mackerel aggregates on the schooled anchovy juveniles, this could be considered an important density-dependent factor in the regulation of the anchovy population. A second phase of this interaction would be if the mackerel population increases in later years as a result of the abundance of anchovy.

Thus we see that marine birds, mammals, and fishes could establish and control growth rates for a clupeoid fish population such as the anchovy. Only in the case of the guanay off Peru (Tovar 1983) and pelican feeding on anchovy juveniles (Anderson et al. 1982) have sufficient data been collected to establish a convincing link to anchovy population control by the mechanism of aggregating or stimulating the population growth of a predator population.

Environmental Mechanisms

The high-seas support no clupeoid stocks in the temperate zone. Usually in the study of the environment of clupeoid stocks we are examining the interaction of the open-sea environment in juxtaposition with the coastal and neritic ones which comprise the clupeoid habitat. The definition and interpretation of these zones must be done with care as exemplified by the writings of Bakun and Parrish (1982), Bernal and McGowan (1981), Chelton (1982), Chelton et al. (1982), Colebrook (1977), Hewitt and Method (1982), Lasker et al. (1981), Owen (1980), Parrish and MacCall (1978), and Smith and Eppley (1982). The mechanism invoked must match the spatial, temporal, and other biological characteristics of the species for which population control is implied. For example, the California Current exhibits laminae of epipelagic fishes in which the clupeoid pair, sardine and anchovy, occupy intermediate areas; onshore are the speciose rockfishes and abundant flatfishes aligned to the bathymetric features of the coast and their interaction with the passing currents. Offshore of the clupeoid pair are the oceanic species of pelagic schooling fish, the jack mackerel (*Trachurus symmetricus*) and the saury (*Cololabis saira*) (Loeb et al. 1983). These are widespread over the transition zone of the Northeast Pacific.

The mechanisms to be discussed below are (1) lethal conditions, (2) biological production, (3) changes in the biological community, and (4) physical and chemical changes in the habitat. Many of the mechanisms to be discussed differ from density-dependent mechanisms only in that the decrease in population growth rate is incidental to the environmental change rather than being a direct result of the interaction of population density and the carrying capacity of the environment.

Lethal temperature, oxygen, etc.

A relatively large fraction of the sardine eggs spawned were placed in sites where the temperature at 10 m of depth (13°C) is known to be lethal to embryonic stages before first-feeding can occur. In 1953, lethal (Ahlstrom 1965) temperatures swept the major spawning grounds of the northern subpopulation of the Pacific sardine (*Sardinops sagax*) and no spawning was detected there. After the warming trend in 1958, virtually all sardine spawning was located in the southern California bight where spawning had previously been excluded. It may be seen that density-independent controls of stock size may be more restrictive to the spawning grounds than the feeding grounds; thus, studies of these features will have to be carefully placed in time and space and be adaptively conducted to estimate the population effect.

Biological production

Based on the early work of Murphy (1966) and Ryther et al. (1971) and later writings by Walsh (1981) and Smith and Eppley (1982), it seems plausible that stocks of clupeoids could achieve sufficient biomass to approach the limits of productivity. Neither the current measures of fish biomass, fish food requirements, nor biological production are adequate to test this hypothesis because the interaction of the disappearance of food and the increased energy of searching for the remainder cannot be studied until a clupeoid population is found whose density is near the carrying capacity. Since the clupeoid populations constitute a significant nitrogen source, the primary limitation on production would be the time between the renitrification of the environment and the elaboration of plankton edible by the clupeoid stock involved. The poleward and offshore migrations of the temperate clupeoids might reflect a behavior brought about by limitations of biological production and the relative standing stocks of food (Lasker 1970) in the two environments. Excellent measures of recruitment would be necessary for detecting subtle effects of limits of biological production; given the mobility of the juveniles at maximum cohort biomass, recruitment failure studies would require intensive regional measures of feeding and food availability.

Biological production is not yet measured routinely over oceanic areas of significant size relative to the distribution of clupeoids. For the most part, secondary production is unmeasureable by present techniques, and the elaborate methods

necessary to estimate primary production in a broad geographic area have defeated attempts to obtain a seasonally and geographically satisfying estimate of primary production in any upwelling coastal area. Eppley et al. (1979) reported the primary production in a small area of the Southern California Bight and Smith and Eppley (1982) compared the time series with that of the northern anchovy biomass in that small area. The main barriers to temporally and spatially coherent measures of primary production are that the primary production will likely be very patchy in space and episodic in time (Tont 1976).

There are some data with which to form plans for studies of primary and secondary production off California. Colebrook (1977) analyzed the CalCOFI biomass data and found a clear pattern for the major elements of the biota. He found that there were two clear planes of variability: one was associated primarily with the California Current and the other was cross-shore near the coast. The organisms associated with the subarctic flow from the transition zone were in the "functional groups" Thaliacea, Siphonophora, and Medusae. Organisms whose orientation was primarily cross-shore were in the functional groups Copepoda, Euphausiacea, and Chaetognatha. Another description of the same data may be found in Fleminger et al. (1974); they described the coastal upwelling as extending the habitats of the temperate ocean toward the tropics adjacent to the coast in a narrow band.

Similarly, in a phytoplankton community study, Malone (1971) described a geographic division oriented to the coast. In the vast majority of the oceanic area and most of the time that the nannoplankton did not dominate was during episodes of coastal upwelling; at that time the production was primarily by large diatoms. Malone found that the geography of the bloom could be described by the presence of chlorophyll *a* greater than 0.5 $mg \cdot m^{-3}$ at the surface. Long time-series of episodic diatom blooms were described by Tont (1981), and the nature of the episodes was described by Tont (1976). Tont found that most of the diatom biomass was detected in three blooms per year and the duration of the upwelling effect was slightly more than 1 mo.

Given these diagnostic features of primary production, the spatial and temporal description of interannual change should be approximated usefully by ships under cloud cover and by satellites when conditions are favorable. Smith and Eppley (1982) found that statistical relationships among the levels of production were exponential. That is, the relationship among primary production, zooplankton volume, and anchovy larval abundance was highly nonlinear. Larval growth and survival and recruitment should be compared with simple indices of the area influenced by upwelling. Alvariño (1980) has already begun the characterization of the spawning habitat in terms of the invertebrate communities there and in nonspawning areas.

Walsh (1981) illustrated the problem with biological productivity measurements by reporting a "time-series" of primary production with a range of 1966 to 1978 off the coast of Peru. He stated that the 1966 values are high because they were taken in a high chlorophyll area at the shelf break and that the 1976–77 data are low because repeated time-series stations were taken within a low chlorophyll area near the coast. This means that 101 of 185 stations are not representative. He failed to mention in the text, but listed in tables, the fact that 149 of the 185 samples reported were taken at 15° south in an area where Santander (1981) showed that there are usually few anchovies. Also, 159 of the 185 samples reported were from February through May and only 4 samples were during the austral winter in August and September. Walsh also chose to calculate an overall average from cruises or citations that varied in number of samples from 4 to 43. Thus, we see that someone constructing a model that includes primary production off Peru is forced to use an invalid set of samples. The average rate of carbon fixation was 3.98 $g\ C \cdot m^{-2} \cdot d^{-1}$. The situation is little better off California where there are many measurements within 30 km of the coast, and 1 yr of primary productivity reported (Owen 1974) with 38 stations spread over 12 mo and 250000 square nautical miles (M^2). Of these, only three were in the habitat of the central subpopulation of the northern anchovy in February–March of 1969, one station in May–June, two stations in August–September, and two stations in November–December.

It would appear from this that it may be some time before a primary production time-series of sufficient extent, coherence, and duration is availalable with which to consider a fundamental property of eastern boundary currents, the habitat of massive clupeoid populations.

Changes in the biological community

Loeb et al. (1983) described the large-scale spatial relationships of the organisms constituting the community that normally contains the schooling pelagic clupeoids, anchovy and sardine, delineating also the offshore, inshore, subarctic, and subtropical boundaries of this community. One may see from the time-series work of Bernal and McGowan (1981) that the relative size of these zones and the clupeoid habitat off California may be quite changeable. Colebrook (1977) estimated that the subarctic boundary and strength of the California Current parallel to the coast was the most important influence on biota and that a second significant plane of variability existed onshore and offshore.

There is frequently little distinction between those changes in the biological community that are brought about by the population in question and those that are merely incidental to other environment changes. For example, if the anchovy stimulated the aggregation and growth of predatory populations in its habitat and these populations grew to control the anchovy, the incidental effect on the cohabitant sardine might well be determined to be density independent. Thus, it is the origin of the change rather than the effect of the change that distinguishes between these phenomena and those described above.

Physical and chemical changes in the habitat

Advection — Chelton et al. (1982) concluded that large-scale variations in the flow of the California Current play the dominant role in controlling zooplankton biomass by advection of nutrients. Their argument is strongly supported by the coherent response of the zooplankton volume over a very large oceanic area (240 × 1000 M) to changes in flow between 1955 and 1959, and supported by the rest of the time-series between 1951 and 1979. Murphy (1966) in his study of the sardine population noted that the annual rate of flow into the habitat was $47 \times 10^{12}\ m^3 \cdot yr^{-1}$ and that the zooplankton transported in was 0.6 $g \cdot m^{-3}$ and that transported out of the California Current region was 0.05 $g \cdot m^{-3}$. He estimated that the imported zooplankton was equal to one standing crop but acknowledged that the species composition was different. Transport over most of the area is simple but a narrow band near the coast is complex (Hickey 1979), and one would need to know the orientation of various phytoplankton, zooplankton, and fish species to these general areas to interpret these results more fully. Haury and Shulenberger (1982) were unable to confirm the nutrient transport hypothesis of Chelton et al. (1982).

Wind-stress curl — Chelton (1982) used the wind-stress curl data assembled and reported by Nelson (1977) to describe a mechanism for the addition of nutrients to the euphotic zone by upwelling in a zone about 60 M offshore. This effect would extend between San Francisco and northern Baja California. No time-series or source water analyses are yet available to evaluate the range of this phenomenon or its effect on zooplankton and pelagic schooling fishes.

Isopycnal shoaling — Isopycnal shoaling is a large-scale effect caused by geostrophic tilting of isopycnals (uplift of entire density structure at coastal margin of gyres). As these isopycnals are inserted into the euphotic zone, productivity is enhanced. When the long-term, large-scale time-series of salinity (Chelton et al. 1982) is compared with advection, it appears that neither horizontal nor vertical advection is dominant for nutrient addition to the California Current. They emphasized that the vertical motion is not due to classical wind-induced coastal upwelling but is associated with geostrophic tilting of isopycnals from large-scale, low-frequency changes in the transport; thus, both horizontal and some vertical advection are caused by the flow of the California Current.

Wind-driven coastal upwelling — Barber and Smith (1980) characterized coastal upwelling ecosystems by several quantifiable features: (1) midwater oxygen minimum layers, (2) highly organic sediments, (3) anoxia, (4) denitrification and hydrogen sulfide events in subsurface waters, (5) large bird populations, and (6) guano deposits.

Source water — The physical introduction of deeper water into the euphotic zone, whether by isopycnal shoaling, coastal wind-driven upwelling, or wind-stress curl, generally has the effect of cooling and adding nutrients. The exceptions are, of course, when the source water is itself warm or nutrient free. Barber and Chavez (1983) emphasized the relationship of the qualities of the source water for upwelling to the response of the euphotic zone.

Since the California upwelling zone is not well defined or as extreme as the criteria established by Barber and Smith (1980), it will be useful to organize some measures that can be estimated from a variety of platforms in addition to the standard surveys. Surface chorophyll *a* in the range 0.5–10 $mg \cdot m^{-3}$ should be a useful boundary feature. Copepod biomass above $10\,g \cdot 1000\,m^{-3}$ in the upper 140 m and euphausiid biomass over $2 \cdot 1000\,m^{-3}$ in the upper 140 m should also serve as ready guides to the outer limit of the upwelling impact zone. Since these macroplankton have taken several weeks (copepods) or months (euphusiids) to respond to the upwelling enrichment, one should not expect these values at the site of upwelling.

Why is the recruitment to the central subpopulation of the northern anchovy so variable? To echo Gulland's (1982) theoretical paper, "Why is the recruitment to the central subpopulation of the northern anchovy not so variable?" At the beginning of the Mechanisms of Population Control section, we posed an extremely simple model of eight arbitrary stages in the anchovy life cycle. Following the lead of Shepard and Cushing (1980), the controlling parameters of each stage were the mortality and growth rates (Murphy 1961) of a stage of fixed length interval. The obvious reason why recruitment can vary is that relatively minor changes in these exponents can singly change the outcome severalfold. If these parameters are correlated with each other in a cohort, their joint effects would be devastating. If the later fate of the cohort is ultimately controlled by the carrying capacity of the environment, some of the early life stage losses or gains could be nullified. If the growth rate and the mortality rate were each adjusted independently and stochastically on a weekly basis, there would be a strong temporal averaging process. Similarly, if weekly cohorts encountered radically different conditions, there would be a second temporal averaging process. Thirdly, if the environment with respect to growth and mortality rate were structured as a mosaic, each sector of which had different rates, there would be yet another averaging process. Thus, we see that the answer to the question of why recruitment is constant is that temporal averaging within each cohort, temporal averaging among cohorts, and spatial averaging all taken together would likely enforce a certain level of stability on the eventual population size. Given the expense of confirming theory, development of predictions, and establishing monitoring systems with which to implement management recommendations (for stocks distributed over thousands of square kilometres of coastal ocean) the practical questions of costs must be raised. This is the subject of the next section.

Evaluations and Predictions

Thirty years ago, the chief problem in clupeoid fisheries was to define the stocks that had not yet been fished. Most of the catch of clupeoids in the past three decades was from stocks that had not yet been evaluated at the beginning of that period. While there are still isolated stocks of clupeoids that have not been fished, their potential yield appears small relative to those stocks that have been fished. Thus, with regard to the biological and economic yield from this taxonomic group, the largest remaining unexploited resource is effective stock management.

The physical yield from the clupeoid stocks may be expected to follow rather simple (Blaxter and Hunter 1982) (even if elaborate in total) biological rules for reproduction and harvest in a varying environment. The economic yield will probably be dominated for some years by increasing values caused by the increase of the human population and the conversion of the catch from relatively low value products of fish meal and oil to higher valued canned and cured products. Restoration of the stocks under the condition of higher demands and higher values is a first management priority. Higher stocks may be expected to yield more for less fishing effort, recover from natural variations faster, and provide other values as forage for coastal birds and migratory predators such as marine mammals and larger fishes.

Clupeoid O-Group Biological and Economic Models

Lenarz (1971) explored some economic consequences of management of the recovery of the Pacific sardine stock and the subsequent long-term yield as a function of the precision of management advice. Characteristics of sardine recruitment elucidated by Murphy (1966) were incorporated into the model. These were the reproductive capacity, recruitment variability, and the tendency for annual recruitment success to be linked with the previous years' recruitments, namely that recruitment failures tended to occur in runs, as did successes. He explored the management tools, quota, and fishery closure. Above a fixed biomass level fishing mortality was controlled and below that level the fishery was closed.

The simulation by Lenarz (1971) did not consider the economic effects of the yield but explored long-term average yield and yield per unit-of-effort as a function of management

policy and the precision of estimates on which the policy was based. The policy of total closure at a fixed biomass increased the long-term yield about 1% but increased the yield per unit of fishing mortality by 0.4. Allowing the upper limit of fishing mortality to rise to 1.05 resulted in small long-term *gains* in average yield but significant *losses* in yield per unit of fishing effort. Precision management to maximize biological yield and yield per unit of fishing effort resulted in a closure of the fishery in 25% of the years for periods up to 4 yr. The quality of the biomass estimates had a moderate effect on yield and yield-per-effort when crude estimates were used, but 10% increases in yield and yield-per-effort resulted from improving the multiplicative error factor from 4 to 1.5.

Huppert et al (1980b) combined a biological model, a biomass-dependent yield-per-effort fishing model, and an economic yield model to explore the benefits of different management policies for the reduction segment of the northern anchovy fishery. They also included stochastic variability in actual recruitment and in the estimation of stock biomass. Their management policy included (among other things) a maximum on total catch and a closure of the fishery when the biomass was below set limits. Their management policy was based on a biomass estimate and they allowed the standard error of estimate to improve from 0.4 to 0.05 (about 2.5 to 1.05 on the Lenarz scale). The cost of the survey was scaled to the sampling effort and cost of a survey using 500 samples (1978 dollars). They assumed that survey costs were proportional to the number of samples and that the standard error of estimate decreased as the square root of the number of samples.

Huppert (1981, p. 73) concluded that the diminishing returns of value from the catch per unit of survey cost became negative between proportional assessment standard errors of 0.30 and 0.25. Further work of a similar nature was used to demonstrate the added value of allocating a portion of the catch based on the spawning biomass estimate and another portion at midyear based on a hypothetical recruitment estimate (Huppert et al. 1980a). They found that a very accurate and precise estimate of recruitment (0.1 standard error as a fraction of the mean) (Anonymous 1983) could augment the spawning biomass estimate usefully only if the annual cost of the recruitment survey was materially less than $\$250\,000 \cdot yr^{-1}$. They did not explore the value of a recruitment survey without a spawning biomass survey.

The scale of the fishery in the work of Huppert et al. (1980a, 1980b) and Huppert (1981) is probably too small to apply directly to the fishery commodities of a global clupeoid fishery, but some dimensions would be interesting to expand to that scale. If we incorporate the data for the Lenarz (1971) model of the value of a sardine recovery and the data from Huppert et al. (1980a, 1980b) and Huppert (1981) for improving the precision of management, we should be able to project the management research and management tactical costs for restoring and sustaining global clupeoid yields.

The expected monetary value for an annual 400 000 t catch of northern anchovy (fished for reduction to meal and oil) is \$4 million, or about \$10 annually per metric ton of yield. Herring have yielded 3 million t for a long period, rose to nearly 5 million t for a brief period, and then fell to 1 million t currently. Anchovies have yielded 15 million t briefly and now yield 2.5 million t. Assuming that the combined restored catch could be approximately 10 million t, the restored values would be \$75 million above the harvesting and processing costs for anchovy and \$20 million for herring.

The additional value of precision management could exceed the costs of the northern anchovy fishery by $\$40\,000 \cdot yr^{-1}$ or $\$0.10 \cdot t^{-1}$ (this assumes an optimum fleet size and processing facilities, and annually adjusted quotas). If all clupeoids were managed this way, and the marginal biological yields were used for meal and oil, the restored 25 million t clupeoid yield would support \$2.5 million from precision management. Thus, the long-term clupeoid yield would have a perpetual expected monetary value of the order of \$250 million annually at 1978 costs and values. Development and implementation of precision management techniques would yield an additional \$2.5 million annually with existing methods.

Bell et al. (1975) project a fivefold increase in price for fishmeal by the year 2000 (approximately 15 yr), and this they projected would accompany a decline in supply from a maximum of 30 million to 15 million t (Anonymous 1982). They also projected a conversion of products from the clupeoid stocks to maintain a level price-function for sardines while doubling the tonnage used to 2.5 million t. Even with the improvement in human fertility trends (Coale 1983), the human population will triple by the year 2100. Thus, we find that the expected monetary values of Huppert (1981) could be a moderate underestimate.

In summary, there has been a transition in research objectives for clupeoid fisheries in the past 30 yr from exploratory fishing to define new stocks to management research to restore depleted stocks and maintain the production of existing stocks. Increasingly realistic biological models of population growth combined with economic models of fishing efficiency and monetary value can assist us in establishing perspective on the perpetual values of existing uses of clupeoid stocks. The most expensive segments for management advice can probably be coupled for several species in the temperate and tropical areas to increase efficiency. The restored biological yield of clupeoids would approach 25 million t, and rise in prices for fish meal and the conversion of end products from clupeoid stocks from meal and oil to canned and cured products will tend to increase the expected monetary values. The projected yield of \$2.5 million from precision management of the restored clupeoid stocks represents the costs and precision of methods as they existed in 1978. It would seem that reduction of costs of management advice is more urgent than increases in precision for sustained management of naturally variable clupeoid stocks.

Recruitment Prediction

Huppert et al. (1980a) evaluated recruitment assessment but did not involve prediction; thus, the economic value of recruitment prediction as a function of lead time and precision has not yet been explored. The values would appear to arise from planning alternate uses for fleet and processing plants during the inevitable closures. Other values might arise from early increases in quotas after the recovery of the stock and earlier closures following the projection of poor recruitment. The research objectives under this topic should involve cost and precision studies of new methods and the merger of recruitment prediction technology and tactics for several stocks in a region, and for the global adaptation of fundamental progress in recruitment studies.

Predictions of stock size in the clupeoids will have three characteristic elements: (1) the size of the spawning stock, (2) the locations, growth, and survival of the juveniles, and (3) the survival rate (R. D. Methot, pers. comm.) and the fecundity of adults. For the purposes of this paper, the sections to follow will

emphasize direct measures of the O-group and environmental influences. The emphasis will be on the development and implementation of low-cost indices of recruitment in clupeoids.

Direct O-Group Studies

Current methods of study of the O-group clupeoid seem confined to labor and ship-time intensive direct sampling; the quality of the samples, in terms of representivity, precision, and accuracy, is in question. The strategy of conversion to lower cost methods rests heavily on the question of when the size of the incoming year-class is determined. It is also possible that the time of recruitment determination changes among years.

A new method for determining the location of juvenile anchovies and directing samples to determine growth and survival has been developed and tested (Hewitt et al. 1976; Holliday 1980). The method consists of three steps: (1) mapping schooled fish targets with conventional sonar, (2) estimating fish size with gas-bladder resonant return of broad-band sound, and (3) trawling to determine species composition. Discrimination of bladder-bearing fish from squid and pelagic crab aggregations is possible, and the length and age of anchovies can be evaluated to a 25-mm length category or 60-d age group for larval and juvenile anchovies between 10 and 110 mm in length. Adult anchovies can be discriminated from the juveniles and larvae, and these latter could be separated into late larvae (10–35 mm), early juveniles (35–60 mm), and late juveniles and prerecruits (60–85 and 85–110 mm, respectively). The precision of the measurements should be within the useful range because continuous line-transect surveys can be partitioned into independent estimates and weighted for representativeness. This method would probably detect recruitment failure and distinguish between moderate and exceptionally large year-classes. Such a method might also replace direct spawning biomass estimates in some years and furnish the continuity needed for management purposes in years when the biomass is too low or so high as not to require direct measures for setting quotas or closures.

Until one knows the success and dependability of the environmental indicators and predictors of recruitment discussed below, it will not be possible to define the direct O-group measurements necessary for perpetual management of clupeoids. It is likely, though, that the current status of O-group direct evaluation techniques will have to be improved to test and evaluate the environmental indices for long-term operational annual recruitment predictions. Thus, the development of direct measures of recruitment will accelerate the postulation (Bakun and Parrish 1982), evaluation (Parrish and MacCall 1978), and implementation of efficient environmental prediction of clupeoid recruitment.

Environmental Prediction of Recruitment

The eventual efficient predictors of recruitment will likely entail inexpensive observations taken at high frequency over vast areas for a multitude of purposes. For the purpose of predicting recruitment the generalized measurement will be evaluated for its effect on growth and survival mechanisms of several categories in the life cycle of clupeoids. Examples of key life cycle events are the successful transition from embryonic to first-feeding larvae (Lasker 1975), maintenance of the feeding larvae in food conditions leading to fast growth and proximity to the juvenile brood grounds (Hewitt and Methot 1982), conversion from carnivory to omnivory at 60 mm for northern anchovy (Methot 1981), and the achievement of maximum cohort biomass (point D in Fig. 3) all in the first year of life.

Clupeoid populations appear to occupy the habitat rather intensely (Ryther et al 1971; Murphy 1966; Lasker 1970; Hunter and Leong 1981; Smith and Eppley 1982; Cushing 1982); thus, measures of primary and secondary productivity could serve to evaluate the timing and intensity of spawning and subsequent survival of growth of the cohort. This approach could be extremely useful where several schooling coastal pelagic species occupy overlapping planktivorous niches. Virtually all the techniques discussed up to now were directed at fishery population management. New economies could be realized by merging measurements for the regulation of multispecies fisheries such as are commonly pursued for clupeoids, scombrids, carangids, and gadoids in the upwelling areas and continental boundary currents.

Environmental measurements may be obtained from standard survey cruises, platform-of-opportunity data, and coastal measures of temperature, salinity, chlorophyll, and sea level. Estimates of temperature and chlorophyll can now be made by satellite or airplane (Lasker et al. 1981; Pelaez and Guan 1982). Large area averages of turbulence, transport, and upwelling can now be obtained from meteorological data fields (Bakun and Parrish 1982). Coastal birds may be monitored for chick production, survival, and growth (Anderson et al, 1982; Tovar 1983) and marine mammals are often monitored (Anonymous 1977). The primary inhibition in the use of the above indicators is that they are more in the realm of individual, intensive, short-term research and they have not yet been forged into the system necessary for effectiveness as a perpetual management tool.

For schooling coastal, pelagic fishes, including the clupeoids, it can be foreseen that the estimation of small-scale spatial intensity of their food will be more important than measurements integrated through depth and space. Holliday (1980) described systems for evaluating forage using multifrequency ultrasound (megahertz), and mergers with pumps and nets are natural applications of this acoustic tool. As in the case of direct measurements of the O-group clupeoids, these techniques will be useful for defining the indicative or predictive indirect measures we need to evaluate plankton composition, spatial pattern and productivity as controls on clupeoid juvenile growth rate and survival and adult fecundity.

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Some Speculations about the Baltic Herring (*Clupea harengus membras*) in Connection with the Eutrophication of the Baltic Sea[1]

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Aneer, G. 1985. Some speculations about the Baltic herring (*Clupea harengus membras*) in connection with the eutrophication of the Baltic Sea. Can. J. Fish. Aquat. Sci. 42 (Suppl. 1): 83–90.

In this paper the hypothesis is put forward that Baltic herring (*Clupea harengus membras*) spawning time, spring or autumn, is determined by feeding conditions during the adult phase and thus not genetically fixed. The present "absence" of autumn spawners is thought to be the result of improved feeding conditions during the latest decades as a result of the eutrophication of the Baltic Sea. During two spawning ground studies carried out in 1978 and 1982 unusually high mortality rates were noted for eggs in situ. In 1982, during 4 wk close to peak of spawning, the mortality increased substantially, especially for eggs among filamentous algae. A significant difference was noted between eggs on coarser algae and those among filamentous algae ($p < 0.001$). During this period the average mortalities were 33 and 75%, respectively. Very low levels of oxygen were measured at night among the filamentous algae. An increase in the amounts of this type of algae as a response to the eutrophication might constitute a new hazard to the reproductive success of the Baltic herring.

Dans le présent document, nous avançons une hypothèse selon laquelle la période de frai (printemps ou automne) du hareng de la mer Baltique (*Clupea harengus membras*) dépend de l'abondance des ressources nutritives pour les poissons adultes et non de facteurs génétiques. En effet, le fait qu'il n'y ait actuellement pas de frai en automne nous semble dû à l'augmentation des ressources nutritives qu'a engendrée l'eutrophisation au cours des dernières décennies. En 1978 et 1982, nous avons étudié deux zones de frai et constaté que le taux de mortalité des œufs, mesuré in situ, était anormalement élevé. En 1982, nous avons remarqué que le taux de mortalité s'était considérablement accru au cours des 4 sem précédent le frai, en particulier dans les algues filamenteuses. Nous avons noté une différence significative entre les œufs pondus sur des algues filamenteuses et ceux déposés sur des algues moins fines ($p < 0{,}001$). Au cours de cette période, la mortalité moyenne était de 33 et 74 % respectivement. La concentration d'oxygène pouvait descendre très bas la nuit dans les algues filamenteuses. La propagation de ce type d'algues par suite de l'eutrophisation pourrait être un nouveau danger pour le cycle de reproduction du hareng de la mer Baltique.

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The Baltic Sea is one of the world's largest brackish water areas, with an area of about 360 000 km^2. The Baltic herring (*Clupea harengus membras*) is found throughout the Baltic Sea. The sea, in its present brackish phase, is relatively young. Around 6000 B.C. its former limnic stage was replaced by a marine phase with higher salinities than today. Conditions similar to those of today did not occur until around 2000 B.C. (Remane 1958). Today, the salinity varies from about 1‰ in the north to more than 10‰ in the southwest, but in any given place the salinity is practically stable. In the Baltic proper, with a surface area of about 200 000 km^2, a pronounced vertical salinity stratification exists with a halocline at a depth of about 60 m. The density gradient between the upper less saline water and the deeper more saline is such that the halocline is virtually impermeable to oxygen. Frequently the oxygen is depleted below the halocline and hydrogen sulfide (H_2S) is produced. During the twentieth century the average oxygen content in the bottom water has decreased, and around 1970 it was close to 0% saturation (Fonselius 1969). Now and then, vast areas (up to 100 000 km^2) are covered by H_2S-rich water. During these anoxic conditions, phosphates deposited in the bottom sediments leak into the water, and during storms, the bottom water is partially mixed with the surface water, especially along the coasts, and nutrients are brought to the surface (Jansson 1978, 1981). At irregular intervals part of the bottom water is renewed through inflows of saline North Sea water of higher oxygen content through the Belts and the Sound in the southwest. These inflows temporarily improve the situation below the halocline until the oxygen again is depleted (Jansson 1978, 1981).

Recent reviews show that the Baltic Sea has clearly been subject to eutrophication (Ehlin et al. 1982; Larsson and Elmgren 1983) but that there is a dearth of reliable information about the effects of eutrophication on most parts of the Baltic

[1]This paper was presented at the International Symposium on the Biological Characteristics of Herring and Their Implication for Management, convened at Nanaimo, B.C., June 20–22, 1983, commemorating the 75th anniversary of the Pacific Biological Station.

environment. The present knowledge of changes in the amounts of zooplankton, for instance, indicates that these have not changed more than possibly by a factor of 2 during the present century (Kostrichkina et al. 1980). A study by Cederwall and Elmgren (1980) showed that as a result of the eutrophication the median biomass of macroinvertebrates above the halocline has increased more than four times since the 1920's. Below the halocline there has been a drastic reduction in biomass down to almost nothing. Indications of biomass increases of benthic macrofauna presented by others for the southern Baltic (Żmudzinski 1976) and for the Gulf of Bothnia (Elmgren et al. 1984) support the results of Cederwall and Elmgren (1980).

During the above-mentioned period the annual catch of Baltic herring increased from about 40 000 t in the 1920's to a maximum of about 450 000 t in 1979 (Ojaveer 1981a; Anonymous 1982). Due to insufficient data it is not possible to state whether this increase is the result of an increase in fish biomass and/or the increased efficiency of the fishery as a result of the gradual introduction of more efficient methods, which has moved the fishery more offshore and increased the total fishing effort.

In the 1920's the herring catches along the Swedish coast were dominated by autumn spawners (Hessle 1925). According to him the autumn spawners made up the greater part of the catches not only in Sweden but also in other countries. Ehnholm (1951) mentioned that catches in the Finnish Quark area were dominated by autumn spawners, at least from the middle of the sixteenth century until the 1950's when the fishing was more concentrated in spring and in the inner parts of the archipelagos. Thereby, a shift took place in the catches from autumn to spring spawners. Today, the catches of autumn spawners are insignificant in the entire Baltic Sea (Anonymous 1982) although they are still present in small numbers.

The Question of Spring and Autumn Spawners

Characteristics Normally Used to Discriminate between the Two Groups

In the following text I use the names "spring" and "autumn" spawners in the way they are normally used by Baltic herring researchers.

On the basis of morphometric and meristic characters, Heincke (1898) divided the Baltic herring into two races, spring spawners ("Strömlinge") and autumn spawners ("Bank herrings"). Among other characters, they differed in the number of vertebrae (VS) and the number of keeled scales between the pelvic fins and the anus (K_2). There is a clinal variation in these characters within the Baltic (Hessle 1925); they have been extensively used for separation of stocks and populations. In general, the values of VS and K_2 decrease from south to north.

There are also differences in the scales and otoliths in herring hatched in the respective seasons (Ojaveer 1962; Kompowski 1973; Ojaveer et al. 1981), which still are used extensively for separating the two spawning groups and their different stocks in some Baltic areas (see Ojaveer 1981a and references therein). This is the case not only in the Baltic but also elsewhere (Lea 1929; Einarsson 1951; Parrish and Sharman 1958; Parrish and Saville 1965). For example, the relationship between the distance from nucleus to the first winter ring and from the nucleus to the second winter ring differs between spring- and autumn-born herring, as the latter do not form any winter ring during their first winter in contrast with the ones born in spring. This means that their first growth zone normally is larger than that of spring-spawned herring.

According to Blaxter (1958) there is a certain plasticity in meristic characters. It is clear that VS is affected by temperature during development and also by other local environmental conditions. This plasticity is well known and has been mentioned by several authors.

Overlaps and Shifts of Spawning Seasons

During my own study of Baltic herring in the Askö area, northern Baltic proper (Aneer 1975a), I found herring of both spawning types. In general, there were few autumn spawners. Interestingly, the presence of mature and ripe herring all through the summer indicated an overlap in spawning season between the groups. A clear indication of overlap was also obtained in my study of fish larvae in the Askö area (Aneer 1979). I constantly found newly hatched herring larvae from May to the end of September (Table 1). The same pattern is also seen in reports by Parmanne and Sjöblom (1980, 1982) on the abundance of what they call spring-spawning Baltic herring larvae in the sea areas of Finland. Anokhina (1971) and Ojaveer (1981b) have reported that mature specimens of both groups can be present on spawning grounds at the same time. Messieh (1972) found a shift of spawning times in Atlantic herring (*Clupea harengus harengus*) in the Gulf of St. Lawrence.

Agreement between Otoliths and Maturity Stages

A sample from a trawl catch taken in the Askö area in November 1971 contained an unusual number of autumn spawners, almost one third, according to the maturity stages of the gonads. With the intention of learning how to use otoliths for separation between spring and autumn spawners, I sent 150 pairs of otoliths from the sample to Dr Popiel at the Sea Fisheries Institute, Gdynia, Poland. There they regularly used otoliths for discrimination of the spawning groups. Upon the return of the examined and classified otoliths it was evident that the results of the otolith study and that of the maturity stages did not agree very well (Table 2). The mismatch was too big to be consistent with the normal variation (Ojaveer 1962; Kompowski 1973). This would mean that the otoliths differed more than they are reported to do on a regional basis. A conceivable reason might be a misinterpretation of maturity stages, but I doubt that.

What Determines the Abundance of Spring and Autumn Spawners?

Ojaveer (1974) concluded that the year-class abundance of spring and autumn spawners is determined by the thermic state of the sea and the regime of enrichment of surface layers in the area of spawning with biogenes. Sjöblom (1978) wrote that the reasons for variations in the abundance of spring and autumn spawners lie in the differing capacities of the larvae to survive the cold winter and to exploit the nutrient resources of the sea. He tried to couple the abundance of autumn spawners in the Baltic with mild winters, which earlier seemed to have favoured the abundance of autumn-spawning year-classes, but in later years mild winters seem to have failed in doing so.

Rannak (1971) described a close correlation between rich spring herring year-classes and extraordinarily strong inflows of North Sea water into the Baltic. Rechlin (1969) found a similar relationship between inflows and the strength of year-classes of autumn spawners. In the North Sea, Cushing (1975) found a

TABLE 1. Numbers of Baltic herring larvae caught in oblique Bongo-net hauls in the Askö area in 1976.

Date	Length groups (mm)					
	5–9.9	10–14.9	15–19.9	20–24.9	25–29.9	30–34.9
April 22	—	—	—	1	—	—
May 4	—	—	—	—	—	1
May 20	130	—	—	—	—	—
June 8	86	—	—	—	—	—
July 2	114	4	—	—	—	—
July 15	209	140	8	1	—	—
July 29	21	72	21	2	2	—
August 11	6	17	32	16	—	—
August 24	25	1	6	14	4	—
September 9	5	9	2	1	—	—
September 23	20	—	2	—	—	—
November 18	—	1	—	—	—	—

TABLE 2. Comparison between composition of a sample of spring (S) and autumn (A) spawners as deduced from maturity stages and otoliths (sample taken November 2, 1971, in the Askö area, northern Baltic proper).

According to otoliths	According to maturity stages			
	S	A	Juveniles	Sum
S	69	28	8	105
S?	8	3	—	11
A	6	8	1	15
A?	6	2	—	8
?	5	5	1	11
Sum	94	46	10	150

close correlation between spawning time and the production cycles in different areas. He formulated the "match-mismatch theory" in which he linked the timing of spawning, annual recruitment, and long-term changes in fish abundance. For the Baltic there are indications that spawning time is not very closely linked to the production cycles (see above).

Despite the "disappearance" of autumn spawners in the Baltic there is no evidence that the feeding conditions for larvae of the respective categories should have changed in such a way that the observed disappearance can be rationally explained.

Seasonal Food Intake and Food Composition

Sjöblom (1978) also discussed differences in main feeding periods for the Baltic herring, which for spring spawners occur in the autumn and for autumn spawners in the spring (Popiel 1951; Ojaveer 1981a). The Baltic herring is generally considered a zooplankton-feeding species (copepods mostly, Ojaveer 1981a) and for young herring, during their first year of life, zooplankton is completely dominant but thereafter its share of the diet generally decreases (Załachowski et al. 1976; Ojaveer 1981a). For the reproductive part of the stocks of herring spawning in spring the main food intake occurs in the autumn, and then the food is dominated by Amphipoda and especially Mysidae (Popiel 1951; Załachowski et al. 1976; Aneer 1980). The latter food group then constitutes between 40 and 50% of the annual food intake according to calculations by the last two authors. The autumn spawners have their most important food intake during spring (Popiel 1951). Unfortunately, the existing studies have been relatively restricted geographically and few recent studies have been published. Investigation covering the food composition all over the Baltic is lacking. In studies carried out in shallow coastal areas (depth < 30 m) zooplankton seem to be most important (Hessle 1925; Ehnholm 1951; Sandström 1980; Enderlein 1981). However, in material from deeper and offshore areas, Amphipoda and Mysidae make up a large proportion of the food (Hessle 1925; Ehnholm 1951; Popiel 1951; Aneer 1975b; Załachowski et al. 1976; Aneer 1980) although Ojaveer (1981a) mentioned that their importance should be less in the open sea compared with that in gulfs.

Effects of Changes in Food Intake

A recent paper by Hettler (1981) showed that in the clupeoid menhaden (*Brevoortia tyrannus*) egg size is possibly connected with food intake. Menhaden fed to satiation three times a day had an average egg diameter of 0.76 mm, while those fed once a day had a mean diameter of 0.67 mm. The results are not entirely clear, as the groups were subjected to somewhat different background conditions. Hempel and Blaxter (1967) showed that Baltic herring spring spawners had smaller eggs than herring from other areas. It has also been shown in a number of studies that egg size is larger and relative fecundity is lower in spring herring compared with autumn spawners (Kändler and Dutt 1958; Parrish and Saville 1965; Anokhina 1971; Bagenal 1973). This is in contrast with what has been shown for salmonids and some other fish groups (Bagenal 1973). If difference in egg size and relative fecundity in herring is coupled to food intake this would imply that autumn spawners have a reduced energy intake in relation to spring spawners. In the 1950's when autumn spawners still were relatively common a study of fat content by Lühmann (1953) did not reveal any marked differences between the groups. No recent studies of fat content in the two spawning groups have come to my attention. According to J. Popiel (Sea Fisheries Institute, Al. Zjednoczenia 1, Gdynia, Poland, pers. comm.), Polish colleagues have found an increase in herring growth over the last decades. This has also been reported for the Gulf of Riga herring (Ojaveer 1976). During these last decades the abundance of autumn

spawners has been drastically reduced (Sjöblom 1978; Weber 1978; Anonymous 1982).

If one analyzes the results of the VPA-analyses for the Baltic herring (Anonymous 1982) it becomes evident that the mean weight per fish in the spawning stocks has increased during the 1970's in all areas but the southwestern where a decrease is noted. On average an increase of about $1\,g \cdot ind^{-1} \cdot yr^{-1}$ is to be found for the entire Baltic although there are differences between areas. Generally, an increase in individual growth could be expected when fishing pressure increases (Botsford 1981). Such an increase was noted in the North Sea before the collapse of the herring fishery. According to the Baltic VPA-analyses (Anonymous 1982) there has been a decrease in the estimated total amount of herring (practically only spring herring). The order of this decrease varies between VPA's but for the 1982 VPA it was around 7% between 1976 and 1981. Looking at the different subareas it is evident that the trend for each of them differs from the others. In some areas there have been strong estimated increases (60%) over the period for which the VPA is valid whereas for others there have been estimated reductions of up to 37%. If one calculates the mean growth increase for subareas with increases and for those with decreases in stock biomass the results are 1.0 and $0.9\,g \cdot ind^{-1} \cdot yr^{-1}$, respectively, for the spawning stocks as specified (Anonymous 1982). During the 1970's the catches increased around 50% up to approximately 450 000 t, but it is also evident that winter nutrient levels have more than doubled between 1965 and 1976 and increased further since then (Larsson and Elmgren 1983).

Some Changes in the Baltic Ecosystem as a Result of the Eutrophication

Larsson and Hagström (1982) and Larsson (1983) discussed the possibility that most of a primary production increase has taken place during the spring bloom. A strong increase in winter nutrient levels has been observed, especially during the 1970's (reviewed in Larsson 1983). However, no direct evidence for an increase in primary production is known; this is most probably a result of insufficient measurements and a forthgoing improvement of methods, which has not yet allowed a long enough series to show any trends (Larsson 1983). Larsson and Hagström (1982) and Larsson (1983) also discussed the possibility that most of the phytoplankton produced during the spring bloom sediments on the bottom without being consumed by zooplankton, as these are relatively scarce at this time of year and do not have their maximum abundance until later on during summer. As a result of this, most of the spring bloom production is utilized instead by macrobenthos (Elmgren 1984). The macrobenthos seem to have changed more than the amounts of zooplankton (Cederwall and Elmgren 1980; Kostrichkina et al. 1980), the former group by a factor of at least 4 and the latter not more than possibly by a factor of 2.

Studies of Genetics

Anokhina (1971) stated that the time of first spawning is not genetically fixed and depends upon the local environmental conditions. Although she had not made any genetic study she also noted that differences in number of vertebrae, scales, and other meristic characters in spring and autumn Baltic herring, together with the peculiarities of the otolith structure, should indicate different conditions of the individual development and that they did not prove the permanency of spring and autumn spawners. Ojaveer (1981b), who also found what he considered to be mature spring spawners among spawning autumn spawners, suggested that for Baltic herring reproductive isolation exists even when mature individuals of different seasonal groups (according to morphometric and meristic characters) mix on the spawning grounds.

Andersson et al. (1981) found significant interpopulational differences in a genetic study of Baltic herring. Kornfield et al. (1982) claimed to have found genetic differences between spring and autumn spawners in the Gulf of St. Lawrence. They stated that the magnitude of differentiation was small and probably of recent common origin. Grant (1984) considered that the above-mentioned heterogeneity in both studies may reflect sampling errors or could be artifacts of statistical analysis. The differences shown by Kornfield et al. (1982) were not consistent from year to year, and based on this and other studies, Grant (1984) concluded that other evidence suggests that time of spawning is not genetically fixed.

Ryman et al. (in press) found remarkably small genetic differences on a macrogeographic scale for Baltic herring of both spawning groups and also between Baltic herring and groups of Atlantic herring. They used starch gel electrophoresis technique with staining for 24 enzymes, and their results indicated that there are no substantial genetic differences of significance between the two spawning groups nor between different groups of spring spawners within the Baltic Sea. The differences were greater within spring-spawning groups than between spring and autumn spawners. A similar study by Grant (1981) showed racial differences in Pacific herring (*Clupea harengus pallasii*) between two geographically separated groups. No similar division of Atlantic herring was found although two weakly differentiated groups were discerned. The difference between these two latter groups was also found in the study by Ryman et al. (in press).

Grant (1984) discussed the low genetical differentiation in Atlantic herring, looking at the historical evolution of the Atlantic area and also upon the effects of population size and gene flow, and commented that the average time to fixation for a neutral mutation should be in the order of tens of million years. He concluded that the 18 000 yr that have elapsed since the last glacial maximum in the North Atlantic Ocean do not mean that a big divergence is to be expected. The last marine phase of the Baltic Sea did not begin until about 6000 B.C. (Remane 1958), and conditions similar to those of today did not take place until about 2000 B.C. The earliest known remains of Baltic herring have been dated to about 2300 B.C. (T. Sjøvold, Osteological Research Laboratory, University of Stockholm, Ulriksdals Kungsgård, S-171 71 Solna, Sweden, pers. comm.). The spawning behaviour of Baltic herring, where no mating seems to take place and both sexes behave similarly and as individuals without any tendency towards cooperation (Aneer et al. 1983), supports the discussion of Grant (1984) and points to the fact that sufficient time for a differentiation has not yet elapsed.

A New Hypothesis

With the indications presented above on (1) uncertainties in the use of morphometric and morphological characters for the classification of spawning groups, (2) the overlap and the long spawning periods, (3) observed shifts of spawning time, (4) the failure to explain the "disappearance" of the autumn spawners with changes in climate, (5) changes in food availability following the eutrophication of the Baltic, (6) a possible link

TABLE 3. Average egg mortality (%) in samples collected in 1982 from filamentous and coarse algae in the Askö area, northern Baltic proper, and test of difference in mortality within and between substrate type and period (Wilcoxon rank-sum test, Lehmann 1975). NS, not significant. Number of samples given in parentheses.

Period	Filamentous algae		Coarse algae
May 17–June 4	8.4 (23)	NS ($p = 0.121$)	3.0 (24)
	$p < 0.001$		$p < 0.001$
June 7–July 2	NS ($p = 0.087$)	74.2 (58) $p < 0.001$ 33.3 (27)	NS ($p = 1.00$)
	$p = 0.001$		$p = 0.037$
July 5–16	28.7 (6)	NS ($p = 0.081$)	14.2 (8)

between egg size and food intake, (7) changes in growth, and (8) genetic similarities, I put forward the hypothesis that the "disappearance" of autumn spawners in the Baltic Sea is caused by improved feeding conditions, especially for the adults, as a result of the eutrophication of the Baltic Sea. The improved and changed feeding conditions mean that most of the reproductive segments of the herring stocks now accumulate energy enough during late summer–autumn to be able to spawn in the following spring and early summer. The "disappearance" of the autumn spawners has been possible due to the absence of genetically fixed spawning groups and of the ability of Baltic herring to change spawning time in response to changes in feeding conditions. The hypothesis differs from most others where spawning time is connected with the larval stages and where spawning time is supposed to be determined by genetic differences between the two groups: spring spawners will always be spring spawners and vice versa.

Egg Mortality

Background

During a study of Baltic herring spawning grounds in 1978, high egg mortalities were noticed in situ (Aneer and Nellbring 1982). In an enlarged spawning study in the same area, the Askö area in the northern Baltic proper, carried out in May–July 1982, high mortalities were noticed again. On closer examination it turned out that the egg mortalities (given as frequency of dead eggs among present eggs) were high in June. It was evident that the mortality was higher in eggs deposited among filamentous algae than among those deposited on coarser algae ($p < 0.001$, rank-sum test, Table 3). Normally, the egg mortality in herring is considered to be less than 10% (Baxter 1971; Hempel 1971). Although high mortalities have been reported they have most often been connected with egg masses several layers thick (Galkina 1971; Birjukov and Shapiro 1971; Taylor 1971; Ojaveer 1981c) and not with relatively sparse occurrences as in the present case, where clumps were seldom found. The observed egg densities corresponded to less than a single layer. The egg mortality did not increase with depth which is contrary to what Taylor (1971) found for Pacific herring eggs.

A coarse division of the samples into groups of samples in different stages of development (cf. Hourston and Haegele 1980) is shown in Table 4. With few exceptions the observed mortalities are relatively evenly spread out between the different stages of development in each week. This indicates that the mortality was not restricted to any specific developmental stage but to all of them, which is partly in accord with the results of Braum (1973). He showed that the sensitivity to low oxygen saturation increases with increasing age of the embryo and that an increase in the level of chronic oxygen deficiency increases the frequency of abnormal embryos and mortality. His study was only carried out at 8°C and a salinity of 15‰.

Filamentous Algae

In my study area the algae *Pilayella littoralis* and *Ectocarpus siliculosus* (the former dominates) nowadays normally cover substantial parts of the available hard substrates, including other vegetation, from early spring until the beginning of June, especially down to approximately 7 m depth (Wallentinus 1979; I. Wallentinus, Askö Laboratory, Institute of Marine Ecology, University of Stockholm, S-106 91 Stockholm, Sweden, pers. comm.). Observations by Stacey and Hourston (1982) and by us (Aneer et al. (1983)) gave the impression that herring prefer to spawn on coarser vegetation in situations where a choice situation was at hand. The results from my 1982 study (G. Aneer, unpubl. data) showed no differences in the degree of cover of filamentous algae on transects with and without spawn for the first and the last period (periods shown in Table 3) whereas there seemed to be a preference for spawning among filamentous algae during the middle period. Although there was a statistical difference ($p < 0.001$, nonparametric G-test, Sokal and Rohlf 1981) between parts with spawn and parts without spawn on transects with spawn, this could be an effect of drift of the algae. In the beginning of June, shortly after biomass maximum (up to > 200 g dry weight$\cdot m^{-2}$, I. Wallentinus, pers. comm.) *Pilayella* sp. begins to be torn loose and is slowly transported downwards, together with *Ectocarpus* sp., by wave action and currents, often in large, partly live, and partly decomposing mats. At night the oxygen content of the water within these mats is often reduced as a result of respiration and decomposition. Measurements of oxygen levels as low as 0.5 ppm O_2 among the algae were obtained shortly after midnight in early July. The corresponding value in the water above the mats was 10.1 ppm O_2. In daytime (10:00), values down to 5.3 ppm O_2 (8.5 ppm O_2 in the free water) were recorded. The period of

TABLE 4. Mean mortalities of Baltic herring eggs in different stages of development (cf. Hourston and Haegele 1980) as observed in samples taken in situ. The presented values (%) are means for samples obtained during the respective week. For each period, second-row values are standard deviations and third-row values denote number of samples. Values in regular type refer to samples from filamentous algae and those in italics refer to samples from coarser algae.

Period (1982)	Temp., surface	Temp., 10 m depth	Approximate age of Baltic herring eggs (h)									
			6–24		24–72		72–150		150		Close to hatching	
May 17–21	10.4	7.5	—	—	—	—	89.5	—	—	—	6.8	—
	1.0	1.0	—	—	—	—	—	—	—	—	—	—
	4	4	—	—	—	—	1	—	—	—	1	—
May 24–28	10.0	8.9	0.4	—	2.6	*0.7*	—	*5.3*	—	—	—	—
	0.7	1.0	—	—	3.0	*0.8*	—	*4.5*	—	—	—	—
	19	19	1	—	13	*12*	—	*12*	—	—	—	—
June 1–4	15.0	9.2	—	—	—	—	9.1	—	—	—	—	—
	1.7	0.8	—	—	—	—	4.7	—	—	—	—	—
	24	24	—	—	—	—	7	—	—	—	—	—
June 7–11	13.4	11.6	—	—	—	—	81.8	*97.5*	75.7	*34.1*	68.2	—
	0.9	1.6	—	—	—	—	13.3	*2.7*	32.6	*14.9*	38.9	—
	35	35	—	—	—	—	3	*3*	4	*2*	9	—
June 14–18	12.9	12.4	—	*3.3*	55.2	*25.6*	—	*66.2*	—	—	—	—
	0.4	0.5	—	*1.5*	31.6	*31.9*	—	*50.5*	—	—	—	—
	23	23	—	*8*	14	*8*	—	*3*	—	—	—	—
June 21–25	13.8	13.0	—	—	77.9	—	—	—	—	—	83.3	*35.8*
	0.5	0.4	—	—	3.0	—	—	—	—	—	21.0	*50.2*
	28	28	—	—	2	—	—	—	—	—	14	*3*
June 28–July 2	14.1	13.9	—	—	—	—	88.3	—	83.6	—	91.4	—
	0.7	0.9	—	—	—	—	—	—	3.8	—	4.5	—
	50	50	—	—	—	—	1	—	6	—	5	—
July 5–9	15.9	14.2	—	—	—	*3.3*	5.6	*4.5*	—	—	—	*100.0*
	1.0	0.7	—	—	—	—	1.6	*3.4*	—	—	—	—
	39	39	—	—	—	*1*	2	*2*	—	—	—	*1*
July 12–16	18.8	15.7	—	—	76.5	—	—	—	4.2	—	—	*0.3*
	1.1	1.9	—	—	7.1	—	—	—	0.8	—	—	*0.6*
	55	55	—	—	2	—	—	—	2	—	—	*4*

highest mortality among eggs coincides with the maximum intensity of spawning in the area (Aneer 1975a).

Increasing Amounts of Filamentous Algae

Haahtela (1981) showed that filamentous algae of the genus *Cladophora* have increased in the archipelago of Turku, Finland, during the last decade. Kangas et al. (1982) have shown how the increase in abundance of filamentous algae in the outer parts of the southern Finnish archipelago most probably has caused a strong reduction in the abundance and biomass of the bladder wrack (*Fucus vesiculosus*), a brown alga, in areas where it earlier constituted up to 99% of the total plant biomass. The results of Kangas et al. (1982) showed that the filamentous algae, mostly *Pilayella littoralis*, which grow epiphytically upon *Fucus* sp. and other hard substrates, have increased considerably. In some places they have increased more than 10-fold. To a large extent, the authors claimed the cause to be the increases in nutrient contents of offshore waters. From the Baltic eutrophication reviews by Larsson (1983) and Larsson and Elmgren (1983) it is evident that the winter values of the nutrient levels in the Baltic proper have more than doubled between 1965 and 1976 and that they have increased further during the last years of the 1970's. Together with some less well-documented reports presented in a review by Wallentinus (1983) this indicates that filamentous algae most probably have increased also in other parts of the Baltic and not only in the Finnish archipelago.

Changes in Baltic Herring Abundance and in Primary Production

The results of the VPA-analyses (Anonymous 1982) for the part of the Baltic proper where my studies were carried out show a negative trend for the recruitment of herring (given as number of O-group fish). It has gradually been reduced from about 10×10^9 in 1972 to about 4×10^9 in 1982. The lowest value, 2.7×10^9 recruits, was estimated for 1978. In 1978, *Pilayella* sp. and *Ectocarpus* sp. seemed to have covered more of the bottom than in 1982 in our study area, according to our subjective impressions during the two spawning ground studies. According to measurements of pelagic primary production in the Askö area (Larsson 1983) the corresponding values for 1978 and 1982 were 160 and 97 $g C \cdot m^{-2} \cdot yr^{-1}$, respectively; this could indicate differences in the production of filamentous macroalgae between the years. However, a linear regression

analysis between primary production and estimated number of recruits (Anonymous 1982) did not result in any clear correlation for the short period 1976–81.

Conclusion

Rechlin (1969) and Rannak (1971) have discussed how inflows of North Sea water into the Baltic favours year-classes of both spring- and autumn-spawned herring by bringing nutrients from the bottom water up to the surface layer, but as far as I know, nobody has hitherto discussed the possibility that an increase in nutrient levels of the magnitude observed in the Baltic could be a problem to the recruitment. The results presented above from my spawning ground study combined with the indications of an increase in the amounts of filamentous algae may mean that the recruitment of Baltic herring is facing a new, hitherto unknown, hazard.

NOTE ADDED IN PRESS: Since this article was written, Sinclair and Tremblay (1983) have presented a new hypothesis to account for the timing of spawning of herring populations. They hypothesized that the timing of spawning of a herring population is a function of the length of time necessary to complete the larval phase and yet metamorphose within the acceptable seasonal envelope.

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Spatial Configurations of Young Herring (*Clupea harengus harengus*) larvae in the St. Lawrence Estuary: Importance of Biological and Physical Factors[1,2]

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Henri, M., J. J. Dodson, and H. Powles. 1985. Spatial configurations of young herring (*Clupea harengus harengus*) larvae in the St. Lawrence estuary: importance of biological and physical factors. Can. J. Fish. Aquat. Sci. 42 (Suppl. 1): 91–104.

The phenomenon of larval retention has recently been identified as central to the structuring of herring stocks. It has been shown that retention of larval fish populations in estuaries is dependent on active vertical migration, the capacity for which develops with growth, but the present study shows that mechanisms for spatial structuring of larval herring (*Clupea harengus harengus*) populations act at the earliest (yolk sac and post-yolk sac) stages. The study was carried out on the Isle-Verte stock of the St. Lawrence estuary in 1981 and 1982. Length–frequencies and tide-related abundance fluctuations suggested that larvae are retained in the study area. As a result, larvae remain aggregated throughout the sampling period of approximately 1 mo. Yolk sac larvae were significantly more abundant near the bottom than in the water column, while post-yolk sac larvae were significantly less abundant in the suprabenthic layer than in the water column. Larvae, being negatively buoyant, tend to sink in slack water but are transported upwards by turbulence resulting from tidal flows. The extent of vertical transport of larvae in the water column is greatest for larvae with lesser specific gravities; specific gravity is at a maximum at hatching and decreases to a minimum at yolk sac absorption. We conclude that larval specific gravity, current velocity, and the two-layer residual circulation are the major factors causing retention and aggregation of larvae.

Le phénomène de rétention larvaire a récemment été identifié comme central à la structuration des stocks de hareng. D'après les études publiées, la rétention des larves de poisson dans les estuaires résulte de migrations verticales actives dont la capacité se développe avec la croissance, mais notre étude suggère que des mécanismes de structuration spatiale de populations de larves de hareng (*Clupea harengus harengus*) agissent aux stades les plus jeunes (à sac vitellin et à vitellus nouvellement résorbé). Le stock étudié en 1981 et 1982 est celui de l'Isle-Verte de l'estuaire du Saint-Laurent. Les fréquences de longueur et les fluctuations d'abondance liées à la marée suggèrent que les larves sont retenues dans l'aire d'étude. Conséquemment, les larves sont agrégées durant toute la période d'échantillonnage, approximativement 1 mo. Les larves avec vitellus sont significativement plus abondantes près du fond que dans la colonne d'eau tandis que les larves sans vitellus sont significativement moins abondantes dans la couche suprabenthique que dans la colonne d'eau. Les larves, de flottabilité négative, tendent à s'enforcer durant l'étale et sont transportées vers la surface par l'action turbulente des courants notamment lors du montant. Le transport vertical des larves dans la colonne d'eau est supérieur pour les larves à faible poids spécifique; le poids spécifique est maximal à l'éclosion et diminue jusqu'à un minimum lors de l'absorption du vitellus. Nous concluons que le poids spécifique larvaire, la vélocité du courant et la circulation résiduelle à deux couches sont les facteurs majeurs causant la rétention et l'agrégation des larves.

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The hypothesis has recently been put forward that herring stock structure is linked to areas of larval retention (Iles and Sinclair 1982). In estuaries, two-layer residual circulation has been suggested to provide a physical mechanism for retention of larvae. Various studies (Pearcy 1962; de Wolf 1974; Weinstein et al. 1980; Setzler et al. 1981) have focussed on retention of larvae both in mixed and in stratified estuaries. Graham (1972) demonstrated active vertical migrations leading to retention of larval herring within the Sheepscot estuary of Maine. However, he added that although residual

[1]Contribution to the program of GIROQ (Groupe interuniversitaire de recherches oceanographiques du Québec).

[2]This paper was presented at the International Symposium on the Biological Characteristics of Herring and Their Implication for Management, convened at Nanaimo, B.C., June 20–22, 1983, commemorating the 75th anniversary of the Pacific Biological Station.

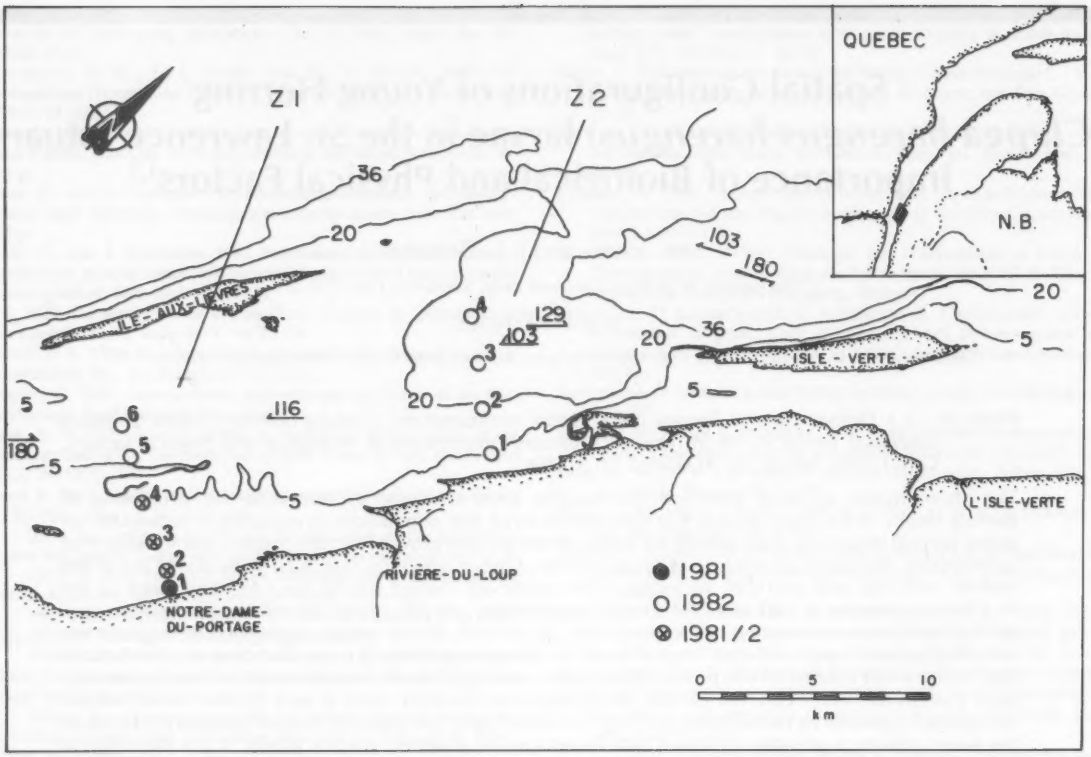

FIG. 1. Study area and sampling stations for the two seasons (1981, 1982). Isobaths (m) and maximum surface currents (cm/s; from marine charts) are indicated.

tidal current affected larval transport, the precise nature of this transport is difficult to determine because of temporal variations in tidal current.

The herring (*Clupea harengus harengus*) stock studied is that of Isle-Verte, characterized by low length-at-age values, possibly a result of slow growth in the first year (Côté et al. 1980). Herring of this stock spawn during the second half of May between Notre-Dame-du-Portage and Isle-Verte (Fig. 1). Several studies have treated distribution, abundance, and transport of larval fishes, in particular herring, in the St. Lawrence estuary. Able (1978) noted that the center of distribution of larval herring moved up-estuary from the presumed spawning ground, over the summer, following spring spawning. Fortier and Leggett (1982) showed that herring larvae were concentrated in the deep layer and carried up-estuary. They proposed that short-term fluctuations in abundance and vertical distribution of larvae should be interpreted in terms of the Fickian representation of transport in partially mixed estuaries (following Fick's law of diffusion of properties along a gradient in a fluid medium).

It has been shown (Graham 1972; Weinstein et al. 1980) that horizontal movements of larvae in estuaries are controlled through vertical migration but that the youngest stages, with very limited swimming capacities, drift passively with currents, as proposed by Fortier and Leggett (1982) for herring larvae < 10 mm. One conclusion might be that larvae disperse after hatching in estuaries until swimming capacities are developed sufficiently to permit vertical migration and, as a result, retention or other spatial structuring of populations. The general objectives of the present paper are to show that the youngest larval stages of herring are strongly retained near the spawning site in a tidally active estuary, and to describe the physical and biological mechanisms that appear to contribute to retention of young larvae.

Study Area

The study area is located in the south channel of the St. Lawrence estuary, between Notre-Dame-du-Portage and Isle-Verte (Fig. 1). The 20-m isobath divides this area into two zones. The first (Z1) is shallow and vertically mixed, while the second (Z2), representing the south channel, is stratified. Two-layer estuarine circulation is a feature of the south channel (d'Anglejan and Ingram 1976); thus, a residual up-estuary bottom current is present here. Surface currents are strong in this area (Fig. 1) and mean minimum and maximum currents at mean depth are approximately 35–67 cm/s (Table 1). Near the south shore of the St. Lawrence estuary, mean current at mid-depths is approximately 20 cm/s down-estuary, in compensation for the mean up-estuary drift in the north channel (Ingram 1979). Maximum tidal fluctuations are approximately 5 m.

Materials and Methods

Field Sampling

Sampling was conducted along a lateral transect of four stations in zone Z1 in 1981 and in zone Z2 in 1982 (Fig. 1). In

TABLE 1. Mean currents (component u (range)) at mean depths (4 m in zone Z1, 14 m in zone Z2) for various tidal amplitudes in the study area.

Area	Date	Mean currents at mean depths (cm/s)		Tidal amplitude (m)
		Ebb	Flow	
Z1	18 June 1981	62 (34–89)	48 (5–81)	3.52
Z1	24 June 1981	58 (8–83)	40 (3–57)	2.87
Z1	2 July 1981	51 (1–82)	58 (26–78)	4.42
Z1	17 June 1982	42 (6–70)	35 (10–55)	3.12
Z1	25 June 1982	56 (2–90)	43 (10–65)	4.17
Z2	11 July 1982	51 (2–120)	62 (38–87)	3.11
Z2	21 July 1982	61 (18–120)	67 (23–96)	4.46
Z2	31 July 1982	37 (14–65)	43 (10–83)	2.36

zone Z1 in 1982, two stations (Nos. 5 and 6, Fig. 1) were added to the transect and the inshore station (No. 1) was dropped. Time series sampling (1-h intervals) was conducted over 13-h tidal cycles at one station in each zone (station 4 in Z1, station 3 in Z2). In 1981, two time series were conducted at neap tides and two at spring tides. A fifth was carried out on 28 June 1981 at station 5 in zone Z1. In 1982, three time series were conducted in each zone. Times of sampling in zone Z1 in 1982 were based on the hatching patterns observed in 1981 and were independent of tidal stage.

On the transects, when depth permitted, an oblique tow was made with a conical plankton net (mouth diameter 0.5 m, mesh 0.333 m) fitted with a General Oceanics flowmeter. Horizontal tows were made at shallow (<2 m) depths. Tows were of 10 min duration at approximately 1.1 m/s (2 knots). Secchi depths were taken following each tow.

On time series stations, an oblique tow and a bottom tow were made hourly for 13 h. In zone Z1 in 1981 and in zone Z2 in 1982, bottom tows were made with a plankton net and in zone Z1 in 1982 with a suprabenthic sled weighing 22 kg and measuring 0.5 m in length, width, and height. The sled was designed to sample at 0.5 m from the bottom. Bottom tows made with the plankton net sampled at approximately 1–2 m from the bottom. Sled samples are hereafter referred to as suprabenthic tows, while bottom plankton net samples are referred to as near-bottom tows. Tows referred to as "bottom tows" are either suprabenthic sled tows or bottom plankton net tows. The suprabenthic sled's plankton net was shorter but otherwise identical to that used for plankton tows. In addition to plankton tows, Secchi disc measurements and hourly current observations at depth were made. Speed and direction of currents were measured five times during 5 min with an Endeco type 1014 current meter. Observations were made at 2 and 4 m at station 4, zone Z1 and at 7, 14, and 21 m at station 3, zone Z2.

Two drogue experiments were carried out. The drogue, constructed of three 1-m-diameter plywood discs fixed perpendicular to each other with a depressor for negative buoyancy, was maintained at 5-m depth and was marked by a lighted buoy. Both experiments began at station 4, zone Z1 (Fig. 1). The first 18 June 1982) lasted 5 h during the ebbing tide. Hourly oblique and suprabenthic sled tows were made near the drogue. In addition, 5-m temperature, Secchi depth, bottom depth, and position were recorded. The second experiment (16–17 July 1982) lasted 32 h. Observations were similar but at 2-h intervals, and the plankton net rather than suprabenthic sled was used for bottom tows.

Laboratory Observations

Herring larvae were counted from fractions containing a minimum of 200 larvae or from whole samples. Presence/absence of yolk sac was recorded. Total lengths were measured to 0.05 mm, on a subsample of 50 larvae in 1981 and 25 larvae in 1982, or the whole sample if numbers were low.

Analytical Methods

The larval abundance index for transects was defined as

$$\frac{\sum_{i=1}^{n} x_i w_i}{n}$$

where x_i = larvae/10 m^2 surface area, w_i = (distance between midpoints of adjacent stations)/(total distance over all stations on the transect), and n = number of stations. The index serves as a weighted average of larval abundance over stations on the transect.

Analysis of time series data from fixed stations was directed at evaluating spatial heterogeneity of larval distributions. Sampling hourly is considered adequate for describing contagious distributions of larvae in tidal current regimes (de Wolf 1974).

The spatial scale of aggregation was estimated to identify the center of the larval concentration in the retention zone. Abundance values (number per 10 m^2) were calculated using the equation described by Smith and Richardson (1977). The patch of herring larvae is presented as though sampling was carried out instantaneously along longitudinal and lateral axes at the end of the ebbing tide. To do this, a part of the time series data (abundance values during either ebb or flood tide) was converted to a longitudinal spatial axis by displacing successive abundance values downstream by distances calculated according to current values measured during the time series. For abundance values measured during ebb tides, the first sample (beginning of ebb) represents the most downstream value. For abundance values measured during flood tides, the last sample (end of flood) represents the most downstream value. To permit incorporation of data from the lateral transects, the abundance values at station 4 in zone Z1 or at station 3 in zone Z2 were interpolated among the time series values on the longitudinal axis. The remaining abundance values from the lateral transect were positioned using tidal displacements relative to the reference station. To detect the center of the larval patch using this procedure, one must obtain a maximum abundance value for both the longitudinal and lateral axes.

The patchiness index used in this study (Lloyd 1967) is derived from an estimate by moments; values of larvae per 100 m^3 replaced the quadrat data usually used to calculate this index. The index measures the intensity but not the spatial scale of patchiness (Hewitt 1981). Since it is independent of mean number per 100 m^3, the index can be used to compare results from periods of different overall abundances. The index was calculated for three data series: oblique tows from temporal series (n = 13), bottom tows from temporal series (n = 13), and all oblique tows including those on the lateral transect (n = 17 for Z1 in 1981 and Z2 in 1982, n = 18 for Z1 in 1982). It should be noted that standard error of the patchiness index cannot be adequately estimated (Lloyd 1967). Thus, statistical comparison of patchiness index values is not possible.

All tow data (number per 10 m^2 or number per 100 m^3) were

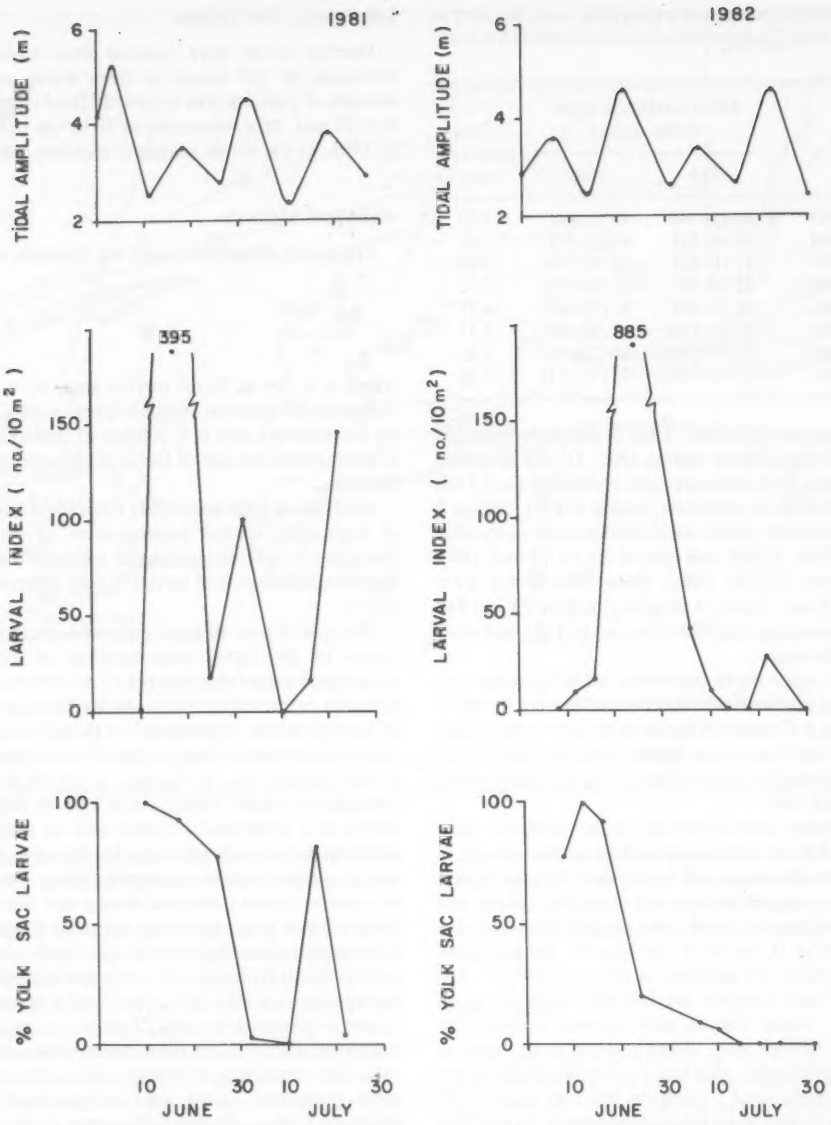

FIG. 2. Fluctuations in tidal amplitude, larval abundance index, and percent yolk sac larvae in zone Z1 for the two sampling seasons (1981, 1982).

transformed by $\log_{10}(x + 1)$, and normality of distributions was verified by the Kolmogorov–Smirnov test prior to carrying out *t*-tests and calculating Pearson correlation coefficients. Ratios of log-transformed abundance values (oblique tow/bottom tow) were used to reduce masking of the vertical component by the longitudinal component when transformed abundance values alone are used. Changes in these ratios with time indicate vertical transport; for example, an increase in the ratio over time indicates upward transport of larvae with time. The role of currents in vertical transport was investigated by correlating current speeds and the ratios of larval densities. Significant positive correlations indicate the transport of larvae from the bottom upwards through the water column with increasing current speed.

Results

Retention

Tide-related abundance fluctuations and length–frequency observations indicate that young herring larvae return with spring tides to the study sites. We observed a relationship between the larval abundance index and tidal amplitude (Fig. 2). For 1981 data, the Pearson correlation coefficient was $r = 0.79$ ($p < 0.05$). Thus, 63% of the variability (r^2) in the larval index was explained by tide. Length–frequencies indicate production of two cohorts, of which the first was still present on 22 July (Fig. 3). Thus, larval growth occurred in zone Z1. The peak in larval abundance index observed 1 July did not result from appearance of a new cohort, since only 2% of larvae had

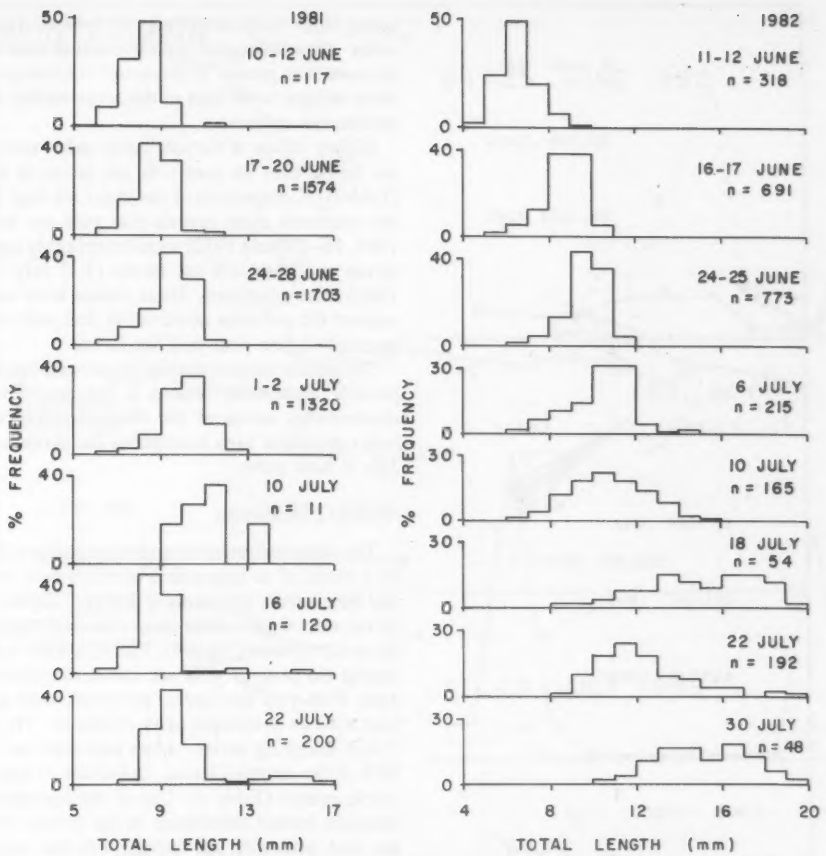

FIG. 3. Larval length–frequencies in zone Z1 for the two sampling seasons (1981, 1982).

yolk sacs (Fig. 2). This peak thus suggests transport of larvae into zone Z1 during spring tides.

In 1982, an abundance peak on 24 June during spring tides was 75% made up of post-yolk sac larvae (Fig. 2). This peak does not appear to result from hatching events as was observed on 18 June 1981. Hatching coincided with spring tide in 1981 but not in 1982. The larval index in 1982 was not significantly correlated with tidal stage ($r = 0.52$, $n = 10$). However, a mean larval index value for the first three cruises was used in calculations, reducing variability due to hatching between 8 and 16 June. Increase in abundance due to hatching could mask the effect of tide in transporting larvae. This mean value is associated with the first period of neap tides. The correlation coefficient became $r = 0.72$ ($p < 0.05$) so that just over 50% of the variability is explained by tide. Length–frequencies (Fig. 3) do not indicate production of a second cohort of larvae in mid-July as was observed in 1981, but these data show that length composition in the area sampled is related to the tide. During spring tides occurring on 10 and 22 July, larvae were smaller than for neap tides occurring on 18 and 30 July.

Return transport of larvae into the area sampled was greater in 1981 (larval index 1 July/larval index 18 June = 0.25) than in 1982 (larval index 6 July/larval index 24 June = 0.05) (Fig. 2). The difference may be due in part to greater tidal amplitudes on 1 July 1981 than on 6 July 1982.

Tide-related abundance fluctuations similar to those observed in zone Z1 were also observed in zone Z2. On 10, 23, and 30 July 1982, tidal amplitudes were 3.11, 4.46, and 2.36 m, respectively, and larval abundance index values were 29, 559, and 27 larvae/10 m^2, respectively. These values were generally an order of magnitude higher than those observed in zone Z1 during the same period. The highest abundance value observed during spring tides on 23 July in zone Z2 was at station 2, whose bottom depth was 20 m. This depth corresponds to the depth of zero residual current in this area (Bio-Conseil 1982).

The results indicate that larvae are retained in the study area despite strong tidal currents. During both years, results demonstrate return transport of larvae into zone Z1 during spring tides. Annual differences in return transport to Z1 were observed. Tide-related variations in length composition for zone Z1 were observed in July 1982. Larval retention appears to be more important in zone Z2, where up-estuary bottom drift occurs, than in zone Z1.

Aggregation

Aggregation of larvae is linked to the phenomenon of retention. Considerable temporal variation of larval abundance in near-bottom water was noted during tidal cycle sampling on 18 June 1981 (Fig. 4). This variation can be interpreted as spatial variability, since different parcels of a moving water mass are sampled over time at the fixed station. The yolk sac stage

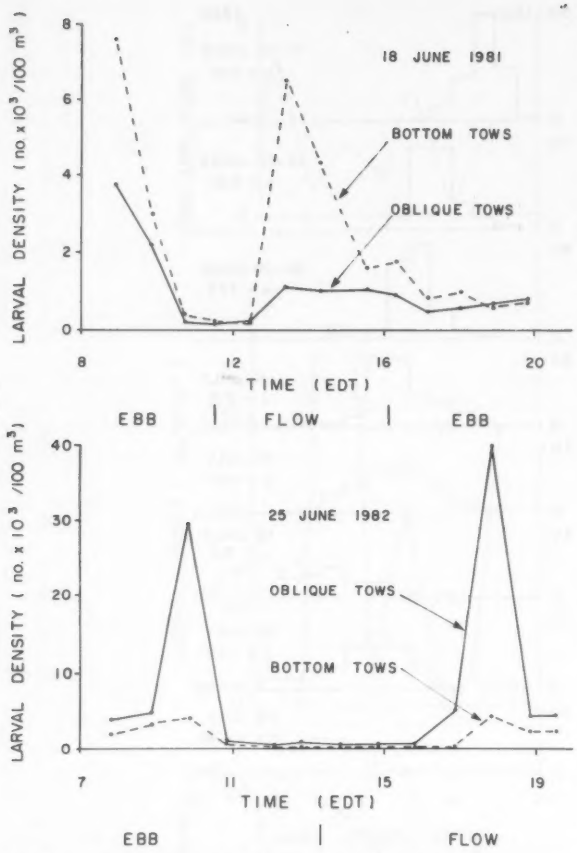

FIG. 4. Larval densities in oblique and bottom tows for two tidal cycles (18 June 1981, 25 June 1982). Bottom tows were made with plankton net in 1981 and suprabenthic sled in 1982.

accounted for 99% of larvae. At first sight, this spatial heterogeneity might appear to result from a discrete hatching event. However, similar heterogeneity was observed on 25 June 1982 for larvae from oblique tows. At this time, only 26% of larvae had yolk sacs. Thus, heterogeneity probably did not result from discrete hatching events but from retention of larvae in a discrete patch and oscillatory transport of the patch with tidal currents.

Data from the two time series conducted during spring tides in 1982 were used to describe the spatial scale of aggregation and to determine the position of the center of the patch of larval herring (Fig. 5). In 1981, the return of larvae to zone Z1 was not sufficient to obtain a maximum abundance value for the longitudinal axis. For 1982, we estimate a down-estuary displacement of the center of the patch equal to 0.2 km/tidal cycle. This rate is 22 times inferior to the rate of displacement of the water mass as estimated by drogue experiments.

In 1981, the patchiness index for 1–2 July was similar to that for 17–18 June, the peak of yolk sac larval abundance (Table 2). Both dates were characterized by spring tides. In 1982, the patchiness index was positively correlated with tidal amplitude (zones Z1 and Z2; $r = 0.93$, $p < 0.05$).

Higher values of the patchiness index were obtained near bottom (plankton net tows) than in the water column during spring tides (tidal amplitude > 3.47 m, Table 2). Patchiness index values increased with increasing tidal amplitude, but the increase was greater in the water column as shown by indices from oblique tows than in the suprabenthic layer as shown by bottom tow indices.

Higher values of the patchiness index were obtained for yolk sac larvae than for post-yolk sac larvae in three of four cases (Table 3). Comparison of the index for total larvae with that of the dominant stage reveals that yolk sac larvae (17–18 June 1981, 16–17 June 1982) were more highly aggregated than total larvae and post-yolk sac larvae (1–2 July 1981, 24–25 June 1982) less aggregated. These values were not independent but support the previous observation that yolk sac larvae are more aggregated than post-yolk sac larvae.

The results suggest that larvae are aggregated by the retention process, apparently related to the deep up-estuary drift that concentrates larvae at the channel entrance. The patchiness index remained high throughout the period mid-June to end of July in both years.

Vertical Distribution

The observed retention and aggregation of herring larvae may be a result of an interaction between their vertical distribution and the currents prevailing at different depths. In 1981, yolk sac larvae were significantly more abundant near the bottom than in the water column (Table 4). The difference was more significant during the peak of yolk sac larval abundance observed on 18 June. Post-yolk sac larvae, however, were as abundant in bottom tows as in oblique tows (Table 4). The value of t for the 2 July sampling series, when post-yolk sac larvae comprised 99% of the sampled larvae, is inferior to that calculated for the whole season (Table 4). Use of the suprabenthic sled in 1982 revealed further differences in the vertical distribution of yolk sac and post-yolk sac larvae. For the entire season, fewer post-yolk sac larvae were observed in the suprabenthic layer than in the water column (Table 4) whereas yolk sac larvae were equally abundant in the suprabenthic layer and in the water column. The same distribution was observed on 25 June during the peak of abundance.

To summarize, the greatest concentrations of yolk sac larvae appear near the bottom with lower concentrations observed in the water column and in the suprabenthic layer. Post-yolk sac larvae appear equally abundant in the water column and near bottom, but less abundant in the suprabenthic layer than in the water column.

Vertical Transport of Larvae

Turbulence created by tidal currents acts to produce vertical transport of herring larvae in the water column. During the flood tide, 83% of the correlations between magnitude of current and the ratios of larval densities between oblique and bottom tows are positive, although only three are significant (Table 5). Since increasing values of the ratio oblique to bottom tow abundance suggest the occurrence of upward transport, positive correlations suggest that degree of transport and current speed are related. No clear tendency exists during the ebbing tide.

The vertical transport of yolk sac and post-yolk sac larvae is different, and many of the nonsignificant correlations are due to the interaction between developmental stage and sampling gear. In 1982, when the suprabenthic sled was used, correlations for yolk sac larvae were significant, suggesting the association between current strength and upward transport (Table 5). As

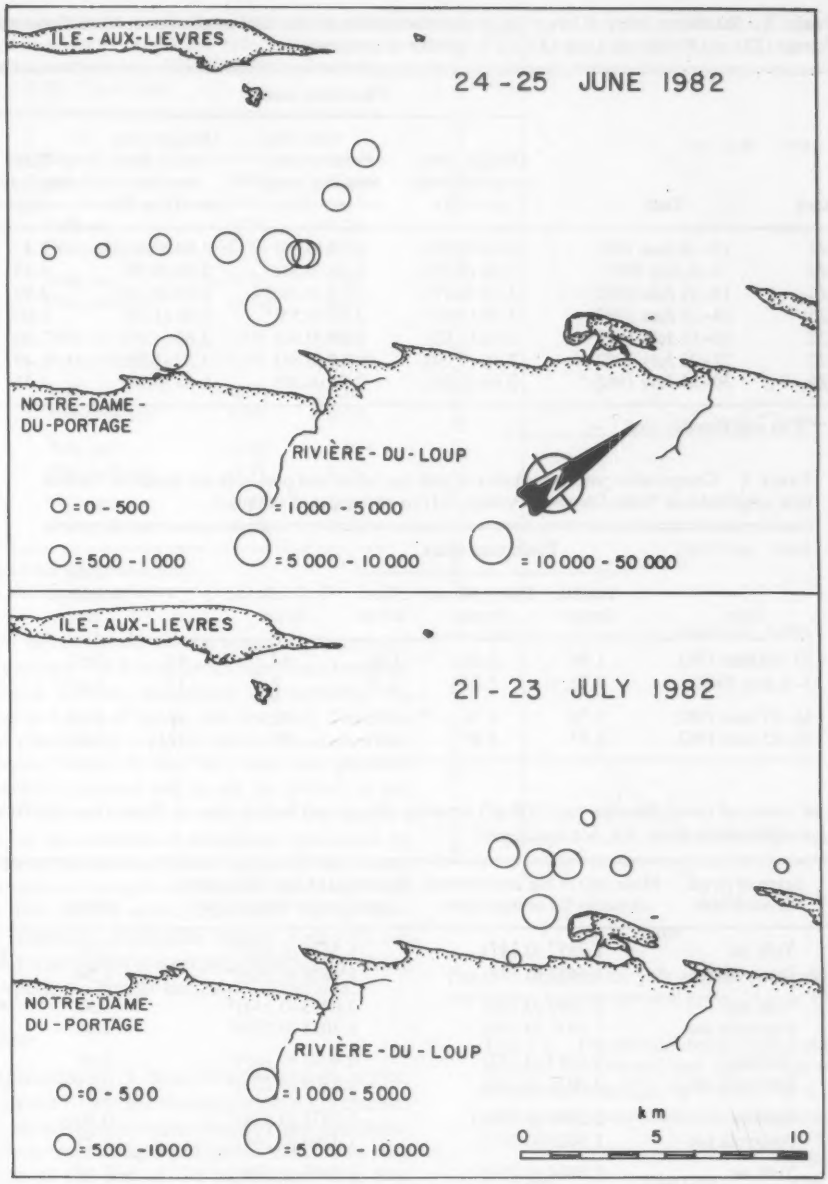

FIG. 5. Spatial scale of larval aggregation for two cruises (24–25 June in zone Z1, 21–23 July in zone Z2) in 1982. Larval densities (no./10 m^2) are indicated by the circles.

post-yolk sac larvae are rare in the suprabenthic layer relative to the water column (Table 4), no significant correlation would be expected between tidal current velocity and the ratio of larvae in oblique tows to suprabenthic tows, and none are observed (Table 5, 1982). In 1981, however, the use of horizontal tows with plankton nets close to the bottom revealed vertical transport of post-yolk sac larvae during flood tides, becoming significant on 28 June when the proportion of post-yolk sac larvae in the sampled population had increased. The failure of horizontal tows close to the bottom in 1981 to reveal vertical transport of yolk sac larvae suggests that although they are transported out of the suprabenthic layer by tidal currents, they nevertheless remain close to the bottom and are not dispersed throughout the water column.

As the vertical transport of post-yolk sac larvae throughout the water column appears more extensive than that of yolk sac larvae, the horizontal dispersion during any one tidal cycle of post-yolk sac larvae should be greater than that of yolk sac larvae. The sampling series of 24 June 1981 supports this hypothesis (Table 5; Fig. 6). A significant vertical transport of post-yolk sac larvae was observed during the ebbing tide (Table 5). At the end of the ebb, few larvae were present, as the patch

TABLE 2. Patchiness index of larvae (SE in parentheses) for various tidal amplitudes at Notre-Dame-du-Portage (Z1) and Rivière-du-Loup (Z2) (n = number of samples).

Area	Date	Patchiness index: Oblique tows, temporal series (n = 13)	Patchiness index: Bottom tows, temporal series (n = 13)	Patchiness index: Oblique tows series and transect (n = 17 or 18)	Tidal amplitude (m)
Z1	17–18 June 1981	2.01 (0.53)	2.29 (0.70)	1.84 (0.42)	3.47
Z1	1–2 July 1981	1.89 (0.45)	2.04 (0.54)	2.24 (0.59)	4.45
Z1	16–17 June 1982	1.38 (0.17)	1.59 (0.28)[a]	1.76 (0.32)	2.92
Z1	24–25 June 1982	3.99 (1.97)	2.06 (0.55)[a]	3.01 (1.25)	4.00
Z2	10–11 July 1982	2.76 (1.03)	1.95 (0.50)	2.86 (1.09)	3.20
Z2	21–23 July 1982	2.86 (1.09)	6.15 (3.84)	3.52 (1.59)	4.49
Z2	30–31 July 1982	2.04 (0.55)	2.04 (0.55)	1.63 (0.27)	2.31

[a]With suprabenthic sled.

TABLE 3. Comparative patchiness index of yolk sac larvae and post-yolk sac larvae for various tidal amplitudes at Notre-Dame-du-Portage (Z1) (n = number of samples).

Date	Patchiness index: Yok sac larvae	Patchiness index: Post-yolk sac larvae	Patchiness index: Total larvae	% of yolk sac larvae	n	Tidal amplitude (m)
17–18 June 1981	1.96	2.81	1.84	93	17	3.52
1–2 July 1981	7.13	2.23	2.24	2	17	4.47
16–17 June 1982	1.79	1.74	1.76	92	18	3.12
24–25 June 1982	4.21	2.83	3.01	25	18	3.82

TABLE 4. Results of t-tests of larval densities (no./100 m^3) between oblique and bottom tows at Notre-Dame-du-Portage (Z1) (n = number of samples, p = probability level, NS, not significant).

Date	Stage of larval development	Mean (SE) of log-transformed densities for oblique tows	Mean (SE) of log-transformed densities for bottom tows	t-value	p	n
Season of 1981	Yolk sac	1.3857 (0.141)	1.5126 (0.152)[a]	2.25	<0.05	51
	Post-yolk sac	1.5634 (0.131)	1.4628 (0.133)[a]	1.54	NS	51
18 June 1981	Yolk sac	2.7392 (0.126)	3.0453 (0.154)[a]	4.55	<0.01	13
	Post-yolk sac	1.5432 (0.196)	1.1015 (0.170)[a]	2.46	<0.05	13
2 July 1981	Yolk sac	0.6147 (0.172)	0.4941 (0.105)[a]	0.68	NS	13
	Post-yolk sac	2.5939 (0.237)	2.5309 (0.233)[a]	0.95	NS	13
Season of 1982	Yolk sac	2.2041 (0.138)	2.1971 (0.134)[b]	0.10	NS	42
	Post-yolk sac	1.9020 (0.183)	1.4293 (0.164)[b]	7.25	<0.01	42
25 June 1982	Yolk sac	2.5884 (0.224)	2.3803 (0.178)[b]	2.17	NS	13
	Post-yolk sac	3.3050 (0.188)	2.5796 (0.221)[b]	6.54	<0.01	13

[a]Bottom plankton net.
[b]Suprabenthic sled.

was located downstream of the station (Fig. 6). During the ensuing flood tide, yolk sac larvae were once again detected in abundance whereas very few post-yolk sac larvae were observed to return within the sampling area (Fig. 6). This supports the deduction that greater horizontal dispersion is experienced by post-yolk sac larvae than yolk sac larvae.

The above observations may be less than conclusive, since correlations are often nonsignificant, but the relationship between upward transport and flood tide current speed is confirmed by examination of information on suspended particulate matter. The Secchi disc readings are inversely related to the quantity of suspended particulate matter. The significant negative correlations observed between Secchi disc readings and larval abundance in the water column and near bottom during the flooding tide (Table 6) support the hypothesis that larvae are vertically transported as is suspended particulate matter and that this occurs principally during flooding tide.

The correlations reported in Table 6 may also have resulted from a decrease in net avoidance by larvae during periods of greater turbidity. If these results are an artifact of net avoidance,

TABLE 5. Pearson correlation coefficients between currents (cm/s; component u at mean depth) and ratio (oblique tow/bottom tow) of larval densities (no./100 m^3) at Notre-Dame-du-Portage (Z1). $*p < 0.05$; $**p < 0.01$.

Date	Stage of larval development	Tidal stage: Ebb	Tidal stage: Flow
18 June 1981[a]	Yolk sac	0.71	−0.28
	Post-yolk sac	−0.35	0.32
24 June 1981[a]	Yolk sac	−0.21	0.02
	Post-yolk sac	0.76*	0.54
28 June 1981[a]	Yolk sac	−0.09	0.50
	Post-yolk sac	−0.47	0.83*
2 July 1981[a]	Yolk sac	−0.60	0.67
	Post-yolk sac	0.45	−0.70
17 June 1982[b]	Yolk sac	−0.30	0.81*
	Post-yolk sac	0.37	0.16
25 June 1982[b]	Yolk sac	0.45	0.94**
	Post-yolk sac	−0.10	0.05

[a]Bottom plankton net for bottom tows.
[b]Suprabenthic sled for bottom tows.

the mean length of larvae should also be negatively correlated with Secchi disc readings. For five of the six significant negative correlations obtained between abundance and turbidity, no significant increase in length of larvae was observed. Thus, we conclude that the relationship between larval abundance and suspended particulate matter is due to a common physical mechanism of vertical transport and is not an artifact of net avoidance.

To summarize, in the absence of turbulence generated by tidal currents, herring larvae are found deeper in the water column. Upward vertical transport of larvae is associated with higher values of tidal current speed, principally during flood tides, similar to suspended particulate matter. Post-yolk sac larvae are vertically transported to a greater extent than yolk sac larvae and thus experience greater horizontal dispersion.

Drogue Experiments

The drogue experiment of 18 June 1982 covered the region between sampling zone Z1 and the entrance to the south channel (Fig. 7a). Significant differences were observed between densities of yolk sac larvae from oblique and suprabenthic tows only during slack water at the end of the experiment (Fig. 8a). However, the increase of yolk sac larvae in the suprabenthic layer was not reflected by a decrease of yolk sac larvae in the water column. This suggests that yolk sac larvae accumulate on the bottom at the entrance of the south channel.

The second drogue experiment resulted in a downstream displacement sufficient to reach areas deeper than 20 m in the south channel (Fig. 7b). A patch of larvae is indicated by three successive peaks of abundance during the first 22 h of the experiment (Fig. 8b). For these peaks, the proportion of larvae on the bottom relative to those sampled throughout the water column increased with time, indicating that larvae were sinking and accumulating close to the bottom as the south channel was approached. Thus, the patch of larvae was drifting at a slower rate than the drogue situated at a depth of 5 m. During the last tidal cycle, the patch of larvae is absent, as the drogue had

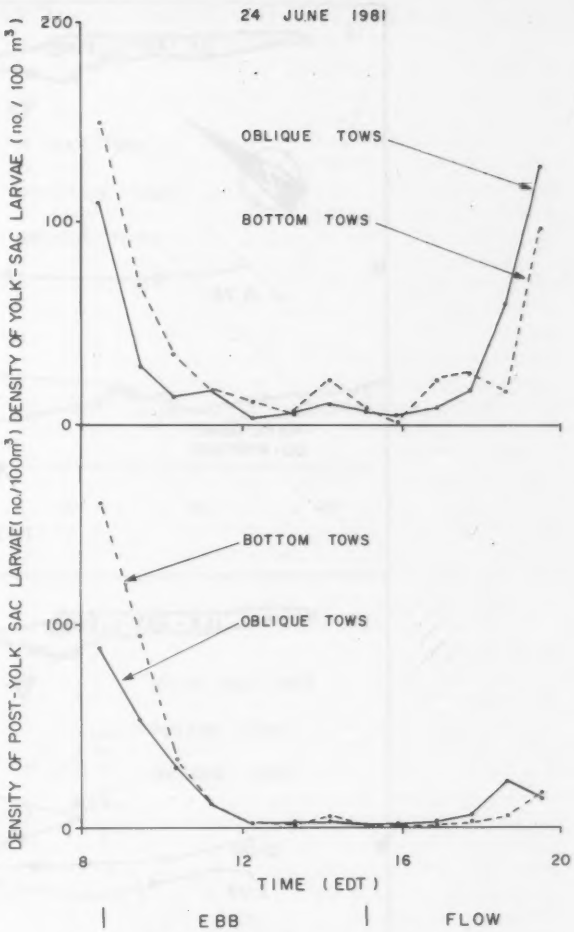

FIG. 6. Densities for yolk sac and post-yolk sac larvae in oblique and bottom tows on one tidal cycle, 24 June 1981.

TABLE 6. Pearson correlation coefficients between larval densities (no./100 m^3) and Secchi disc readings (m) at Rivière-du-Loup (Z2). $*p < 0.05$; $**p < 0.01$.

Date	Tow type	Tidal stage: Ebb	Tidal stage: Flow
11 July 1982	Oblique	0.25	−0.85*
	Bottom	−0.19	−0.86*
21 July 1982	Oblique	−0.46	−0.74*
	Bottom	−0.55	−0.70
31 July 1982	Oblique	−0.78*	−0.97**
	Bottom	−0.55	−0.83*

drifted farther downstream than the patch. The net movement of the drogue was approximately 8 km/d. In less than 4 d, the drogue would have drifted out of the coastal zone whereas the larvae had already been retained in the zone for approximately 1 mo.

To summarize, data from the first drogue experiment sug-

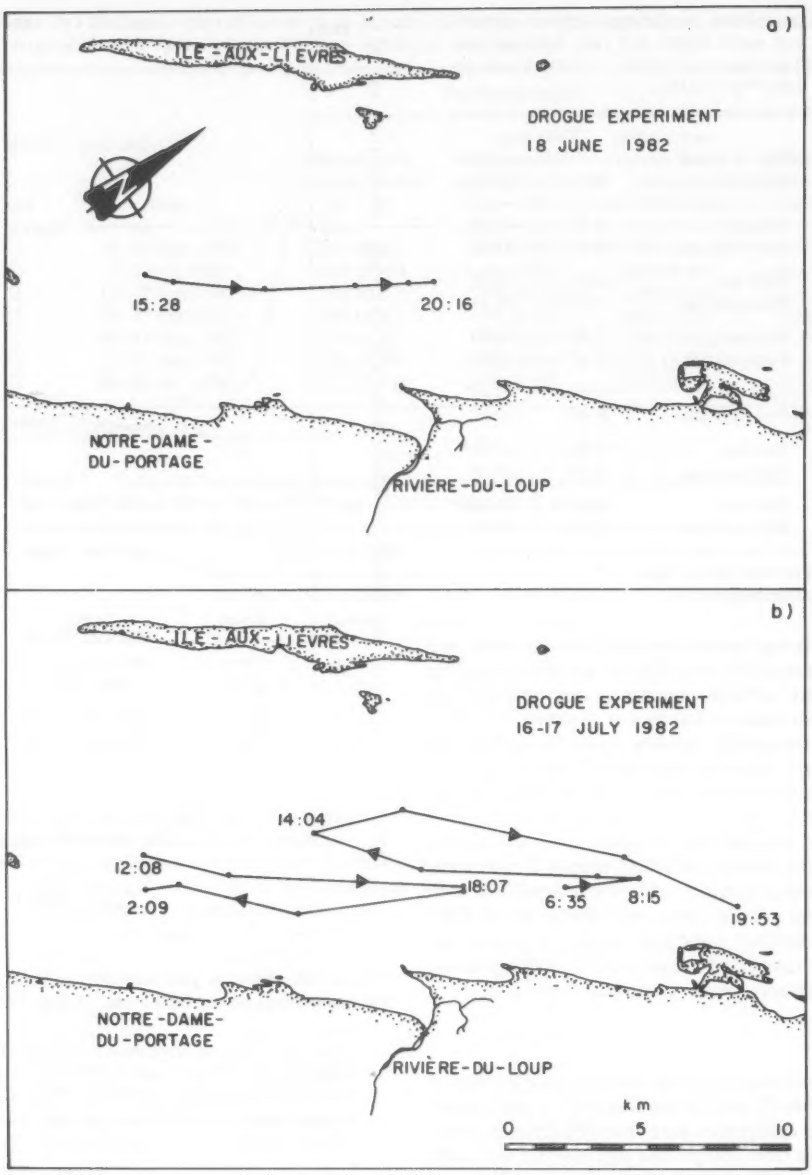

FIG. 7. (a) Drogue trajectory (5-m depth), 18 June 1982. (b) Drogue trajectory (5-m depth), 16–17 July 1982. Discontinuity due to temporary loss of drogue for 4 h.

gested the accumulation of yolk sac larvae on the bottom at the entrance to the south channel. The experiment was of too short a duration to detect any significant changes in the vertical distribution of yolk sac larvae during their transport. The second drift experiment clearly demonstrates the increasing depth distribution of post-yolk sac larvae during their displacement from the coastal zone towards the south channel.

Discussion

The greatest concentrations of yolk sac larvae were found near the bottom in the present study. Several authors (Tibbo et al. 1963; Schnack and Hempel 1971; Caddy and Iles 1973; Colton and Green 1975) have either observed or proposed that yolk sac herring larvae are associated with the bottom. Graham and Chenoweth (1973), on the other hand, found no relationship between the relative abundance of yolk sac larvae and depth. However, their sampling program involved oblique tows at the surface, at 20 m, and at 30 m whereas maximum depth in the study area was 48 m. Saville (1971) suggested that standard plankton nets do not representatively sample the entire water column. In the present study, the use of the suprabenthic sled

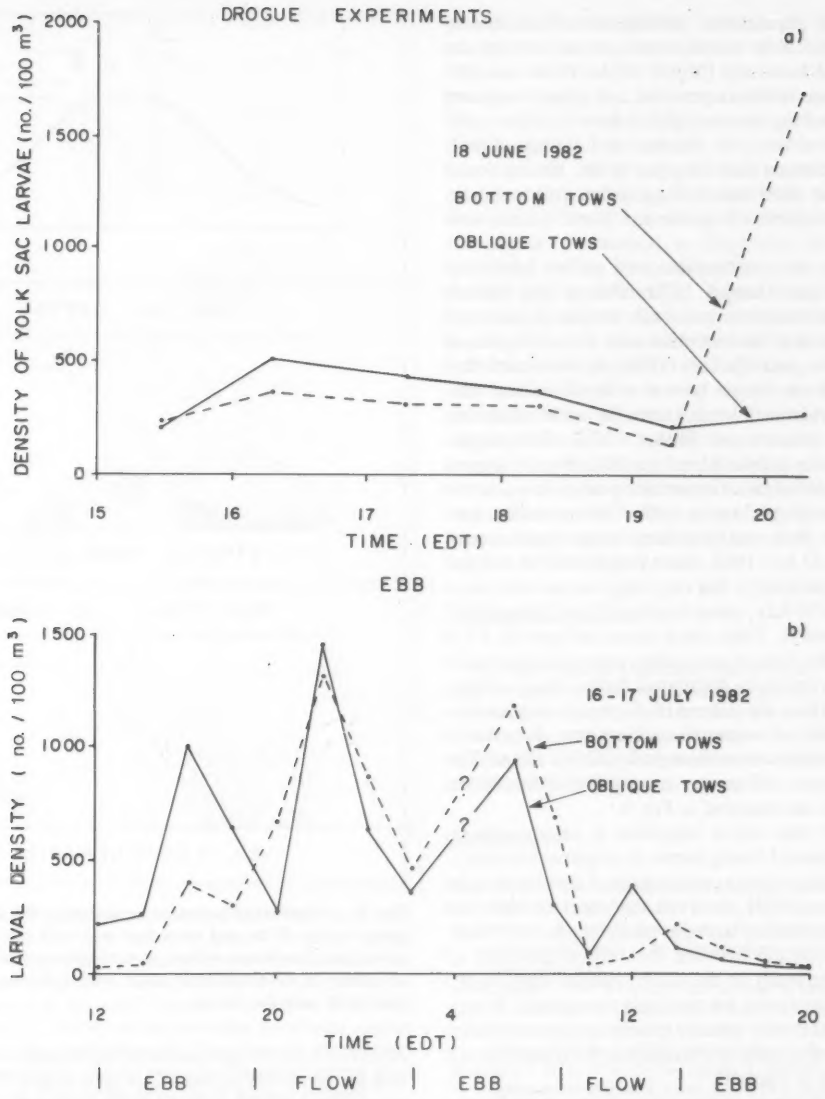

FIG. 8. (a) Densities of yolk sac larvae in oblique and suprabenthic sled tows for drogue experiment, 18 June 1982. (b) Densities of larvae in oblique and bottom plankton net tows for drogue experiment, 16–17 July 1982. Question marks are for period of temporary loss of drogue.

demonstrated the importance of sampling the suprabenthic layer to detect variations in the distribution of yolk sac larvae near the bottom.

While several factors might contribute to this vertical distribution pattern, we believe that negative buoyancy is particularly important. Rosenthal and Hempel (1970) determined that the sinking rate of yolk sac larvae varies between 0.2 and 0.5 cm/s; the larger the yolk sac, the greater the sinking rate. Larvae sink during periods of inactivity that range from 60% of the time for 1-d-old larvae to 34% of the time for immediate post-yolk sac larvae (Rosenthal and Hempel 1970). Therefore, sinking rate varies from 10.8 to 2.9 m/h from the beginning to the end of the yolk sac period. Thus, in the context of the present study such vertical displacements during periods of slack water are significant relative to depths of 7–25 m found in the study area.

The apparent relationship between upward vertical transport and current speed is similar to that shown by de Wolf (1974), who observed a sinking rate of cypris larvae (*Balanus crenatus*) comparable with that of yolk sac herring larvae. In the laboratory, de Wolf (1974) observed upward vertical transport of cypris larvae at current speeds of 35–67.5 cm/s. The range of mean current speeds at mean depths during flooding tides in the study area (35–67 cm/s, Table 1) is comparable with the range noted by de Wolf (1974).

While earlier studies have shown that the yolk sac plays an important role as a regulator of specific gravity, our results suggest that this function of the yolk sac contributes to spatial

structuring of larval populations. Sinking rate diminishes as water content of the yolk sac increases accompanying the absorption of yolk (Blaxter and Ehrlich 1974). Water and lipid diminish sinking rate whereas proteins and sugars augment sinking rate. For herring larvae, lipid content is only 1–3% of the total weight of the yolk (Blaxter and Hempel 1966). Although lipid globules are found in other larvae, herring do not possess them. These observations suggest that yolk sac composition may have evolved in response to a "need" for negative buoyancy.

Our observations, in combination with earlier laboratory studies (Rosenthal and Hempel 1970; Blaxter and Ehrlich 1974), suggest that immediate post-yolk sac larvae are more subject to transport out of the retention area than younger and older larvae. Blaxter and Ehrlich (1974) demonstrated that immediate post-yolk sac larvae have a minimal sinking rate. Sinking rate increases from 0.2 to 1.4 cm/s for larvae measuring from 12 to 25 mm (Blaxter and Ehrlich 1974). Our length–frequency observations in zone Z1 in July 1982 (Fig. 3) suggest that the center of distribution of immediate post-yolk sac larvae (lengths approximately 10 mm) is farther down-estuary than that of larger larvae. Both small and large larvae were taken at spring tides (10 and 22 July 1982, mean lengths 10.7 ± 1.6 and 12.3 ± 1.9 mm, respectively), but only large larvae were taken at neap tides (18 and 30 July, mean lengths 15.0 ± 2.3 and 15.2 ± 2.0 mm, respectively). Thus, since return transport to Z1 is greater on spring tides than on neap tides, immediate post-yolk sac larvae must on average be distributed farther down-estuary than larger larvae. Thus, the pattern of dispersion is related to sinking rate. At minimal values of sinking rate, dispersal is greatest; this characterizes immediate post-yolk sac larvae. The observed developmental differences in vertical distribution and vertical transport are summarized in Fig. 9.

It seems unlikely that active migration is as important a contributor to retention of young larvae as negative buoyancy. Active migration requires that a certain stage of development be attained. Seliverstov (1974) observed the onset of circadian vertical migrations in herring larvae at mean lengths of 13 mm. Moreover, the relationship between the vertical transport of herring larvae and turbidity in the south channel supports the hypothesis that herring larvae are passively transported. Pearcy (1962) was the first to invoke specific gravity as a passive factor to explain why several organisms classified as planktonic are not entirely at the mercy of currents.

The aggregation of larvae remains intense in our study area during the summer months. A coefficient of dispersion (c) between 0.1 and 0.2 is frequent for planktonic population (Cassie 1959), and a patchiness index ($c + 1$, Lloyd 1967) of 1.1–1.2 was considered plausible for herring larvae. Values for patchiness index in the present study ranged from 1.63 to 3.52.

The following description is presented as a model to explain and illustrate the dynamics of the Isle-Verte retention zone. The 20-m isobath appears to be, on average, the up-estuary limit of the retention zone (Fig. 10). As such, it may also represent a preferred zone of egg deposition. During spring tides, the greatest concentrations of herring larvae are found at the entrance to the south channel. Larvae are also found up-estuary in zone Z1. Vertical transport during flood tides appears responsible for this up-estuary transport, the extent of which varies according to the magnitude of tidal speed and the developmental stage of larvae. Horizontal dispersion is less for larvae with greater specific gravities.

Following the maximum of spring tides, larval patches are observed to have experienced net downstream transport. Larvae sink progressively as zone Z2 is approached, their net displacement over one tidal cycle becoming nil once a depth of 20 m is attained. Larvae found at depths greater than 20 m are transported up-estuary by the deep residual current characteristic of zone Z2. This residual current, however, cannot be responsible for the up-estuary transport of larval patches into the relatively shallow and vertically mixed zone Z1. The specific gravity of the larvae should be great enough to minimize down-estuary transport during ebbing tides. Deep currents experienced at the beginning of the flooding tide vertically transport larvae that are subsequently displaced up-estuary. As such, these larval patches return to zone Z1 after having lost a proportion of their numbers to dispersion out of the coastal retention zone and to natural mortality.

Thus, although yolk sac larvae are probably not characterized by strong directed swimming powers, they are not strictly comparable with passive components of the estuarine environment as proposed by Fortier and Leggett (1982). Rather, the presence of a negatively buoyant yolk sac, whose effect decreases with larval development, combines with the inter-

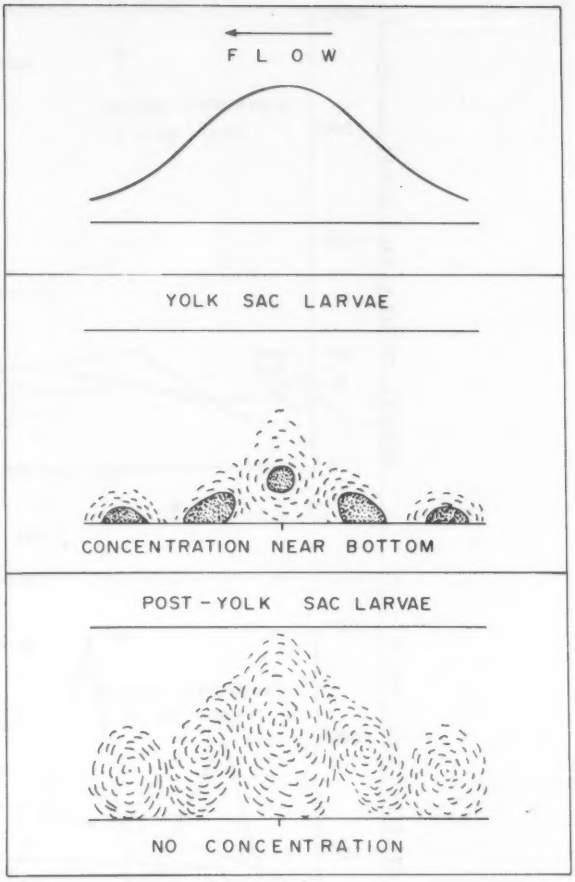

FIG. 9. Schematic illustration representing the differential vertical transport of yolk sac and immediate post-yolk sac larvae. Differences in vertical distribution reflect vertical transport of larvae that varies according to developmental stage with yolk sac larvae associated principally with the bottom.

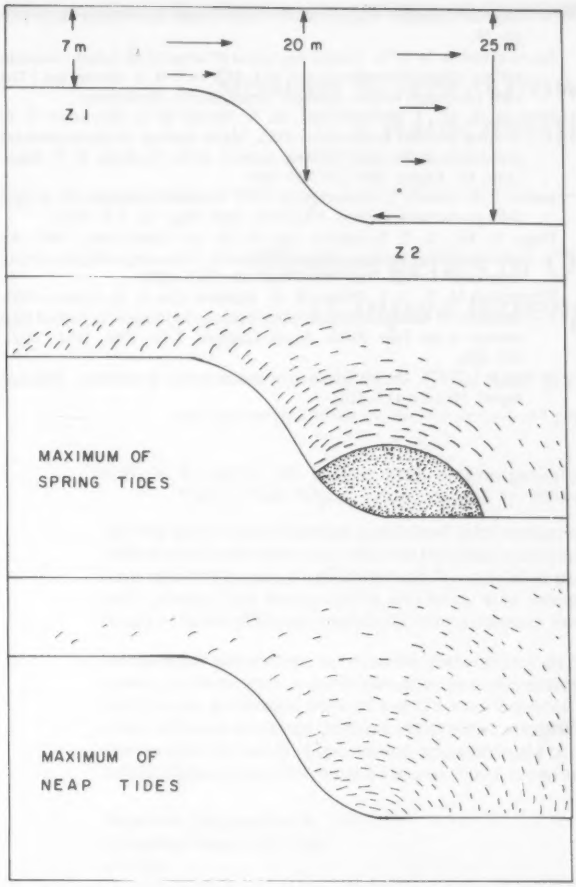

FIG. 10. Schematic illustration representing the model explaining the dynamics of the Isle-Verte retention zone. The 20-m isobath appears to be, on average, the up-estuary limit of the retention zone. During spring tides, the greatest concentrations of herring larvae are found at the entrance to the south channel. Larvae are also found up-estuary in zone Z1. Vertical transport during flood tides appears responsible for this up-estuary transport, the extent of which varies according to the magnitude of tidal speed and the development stage of larvae. The arrows indicate the direction of residual currents.

section of the level of no net motion with the bottom to contribute to strong spatial structuring of larval populations rather than to random dispersal of yolk sac larvae. Our results suggest that the degree of retention is least for immediate post-yolk sac larvae; increased dispersal at this stage may be the result of minimal specific gravity of these larvae and the fact that swimming capabilities are relatively little developed at this stage.

The present study has raised several hypotheses that merit study in the future. Annual differences in the fluctuations of the larval index may be due to an interaction between temperature and tidal stage that acts to modulate the dispersion of larvae in the study area. Temperature influences the date of spawning (Messieh and Moore 1979) and the duration of egg incubation (Blaxter 1956) and therefore influences the date of hatching. The extent of larval retention or dispersion will depend on tidal stage during hatching, particularly if hatching occurs in a short period of time. Laboratory experiments demonstrate that the majority of herring larvae hatch within a period of 3 or 4 d (Blaxter and Hempel 1963). Tibbo et al. (1963) observed patches of newly hatched larvae indicative of waves of hatching separated by 3 or 4 d and correlated with waves of spawning. Observations of the schools of Isle-Verte herring spawners (Bio-Conseil 1982) suggest that peaks of yolk sac larval abundance observed in 1981 and 1982 were associated with individual peaks of spawning. Therefore, we hypothesize that the degree of retention or dispersion of each year-class of Isle-Verte herring larvae depends on the tidal state occurring during rapid mass hatching. As the exact location of egg beds in our study region is unknown, no bottom temperatures were measured and we are unable to develop this hypothesis further.

Increased dispersion at the beginning of exogenous feeding may be considered as having survival advantage by increasing the probability of encounter with food patches. However, increased dispersion leading to premature transport out of the coastal zone may reduce the probability of survival, as food may be less available in deepwater areas than in shallow coastal zones (Pearcy 1962). The optimal equilibrium between dispersion and aggregaton leading to maximum survival must be the subject of future study.

Acknowledgments

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Session 3: Age, Growth, and Reproductive Characteristics of Herring

Bioenergetics of O+ Atlantic Herring (*Clupea harengus harengus*)[1]

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Kerr, S. R., and L. M. Dickie. 1985. Bioenergetics of O+ Atlantic herring (*Clupea harengus harengus*). Can. J. Fish. Aquat. Sci. 42 (Suppl. 1): 105–110.

On the basis of the limited published information on herring bioenergetics, together with general considerations from other species, we propose a preliminary bioenergetic model for Atlantic herring (*Clupea harengus harengus*). Application of the model to published data for five larval cohorts from each of two years shows that temperature and body size interact with the apparent availability of suitable prey to result in quite different metabolic environments that support relatively uniform growth.

Les auteurs présentent un modèle préliminaire de la bioénergétique du hareng de l'Atlantique (*Clupea harengus harengus*), à partir des données restreintes publiées sur la bioénergétique du hareng et de considérations générales portant sur d'autres espèces. L'application du modèle aux données publiées sur cinq cohortes larvaires de deux différentes années montre que la température et la taille corporelle ont une incidence sur la disponibilité apparente de proies adéquates, ce qui entraîne des environnements métaboliques très différents à l'appui d'une croissance relativement uniforme.

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Fisheries bioenergetics is a rapidly maturing field, in terms of the models available for use, and in terms of the detailed observations becoming available for some species. An example of the latter is Brett's (1983) account of the lifetime bioenergetic characteristics of the sockeye salmon (*Oncorhynchus nerka*). An encouraging development, with general implications for the validity of bioenergetic models, is the careful evaluation, using independent test data, provided by Rice and Cochran (1984). Their results indicate that bioenergetic analysis is both a useful procedure and, where sufficiently reliable data are available, a valid procedure.

Herring Bioenergetics

In this paper we are interested in what application of bioenergetics considerations could show about the place of herring in temperate marine ecosystems and how such knowledge could affect the overall aims of management. We approach this objective by making comparisons among various cohorts of larval Atlantic herring (*Clupea harengus harengus*) spawned in two seasons in the southern Gulf of St. Lawrence. Unfortunately for present purposes, neither the herrings nor the clupeoids in general have received sufficient attention to permit bioenergetic analysis that is either detailed or rigorous. The available bioenergetic information for herring has recently been reviewed by Blaxter and Hunter (1982) and Sharp (1980) and will not be repeated here in any detail. It is sufficient to note that the preponderance of work has been on eggs and early larvae, using a variety of techniques that make comparisons difficult, and yielding results that are sometimes in substantial disagreement.

Reasons for the relative lack of development of herring bioenergetics are apparently partly historical and partly due to the biological characteristics of herring themselves. Ecological bioenergetics, with some notable exceptions, was first developed for freshwater and anadromous species and communities, and interest in its application to marine systems is comparatively more recent and therefore less developed. In general, it is true to say that such basic relationships as body weight–metabolism, temperature–metabolism, and like functions are either unmeasured or poorly determined for most major components of marine fish communities. Moreover, many important marine species, herring for example, school from an early age, making it very difficult to devise laboratory procedures for respirometry and other physiological measurements that truly reflect natural rates. It is to be hoped that the deficiencies in requisite

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information for marine species will be overcome, because bioenergetic analysis is of particular importance in understanding interaction in multispecies fisheries. For example, bioenergetic measurements may provide a ready index of the importance of relative abundance changes in cases of shared prey resource requirements or can be used to measure changes in production efficiency with secular changes in environmental variables such as temperature. Herring have long been considered a key species in temperate ecosystems, and particular interest attaches to such studies for them.

Apart from the direct management importance, bioenergetic analyses of herring ought additionally to be ecologically interesting because of their discrete feeding and reproductive behaviours in an annual cycle. Atlantic herring form spawning groups from spring through autumn, spawning in waves roughly 3 wk apart in St. George's Bay (Lambert et al. 1982a). Reasons for the separation between groups were suggested by Ware and Henriksen (1978). Since herring do not feed during gonad maturation and spawning, relying on stored body reserves during the reproductive phase (Iles 1965), the successive spawning groups experience seasonally different environmental conditions such as temperature, and different prey availabilities owing to the seasonal zooplankton cycle, during their individual feeding and growth phases. Similarly, the larvae ensuing from the different seasonal spawning groups experience comparable variation in food availability and temperature. Few species are so discrete in their separation of growth and reproduction, suggesting that herring may be a particularly appropriate species for analysing reproductive tactics. Some preliminary explorations in that direction are offered by this analysis.

A Bioenergetics Model for Herring

All fisheries bioenergetics models are based on a mass balance equation and are therefore fundamentally similar. Apart from structural differences adopted for convenience of application to the available data, the only major difference is in the way that activity metabolism is estimated. Activity metabolism, the difference between actual metabolic rate and certain fixed basal and calorigenic costs, is due to the variable costs associated with growth, reproduction, and other activities, of which on an annual basis the metabolic cost of swimming is presumably the largest. Activity metabolism in nature is virtually impossible to observe directly and so some indirect estimation procedure must be used.

Earlier models, following Winberg (1956), assumed a fixed level of active metabolism, at twice the standard level. Kerr (1971) and Ware (1975) concluded that activity metabolism was variable although most often within the range of 2 to 3 times the standard level. Subsequent models by Kitchell et al. (1977) and Rice and Cochran (1984) have used fixed levels for activity metabolism, but the latter authors introduced variability by finding that several different phases of activity level through the seasonal cycle were sufficient to account for their data. Majkowski and Waiwood (1981) and Kerr (1982), on the other hand, treated activity metabolism as a continuous variable.

For our choice of a bioenergetic model with ensuing assumptions about activity metabolism, we use the model of Kerr (1982). The specific assumption this entails is that growth rate and activity metabolism are directly coupled in linear fashion, a not unreasonable assumption considering the linearity of metabolism and ration at submaximal activities (Brett and Groves 1979). For reasons set out by Kerr, the model is thereby constrained to generate estimates of metabolism that will tend to mimic actual levels, even if the underlying linearity assumption is not strictly met.

More serious than this assumption of the model is the relative weakness of the information available to derive parameters for it. We do not have great confidence that the estimates set out in Table 1 adequately reflect absolute values that characterize herring. For that reason, we do not attempt comparisons of our calculated values for herring bioenergetics with other species. We restrict our analysis in what follows to time-series comparisons within the species, in the belief that absolute errors in parameter estimates do not vitiate comparisons of relative values within and between seasons for the same species.

The model we use (Kerr 1982) is of the form

$$(1)\quad \tau R = \frac{(\tau R_M - T_S)\Delta W}{pR_M - T_T} + T_S$$

where R is ration per fish per unit time, $\tau = p - m$ is a presumed constant conversion efficiency between ration and the energy available for activity and growth (see Table 1), T_S is standard metabolic rate, T_T is maximum sustained metabolic rate, and ΔW is the rate of surplus energy accumulation (which includes both somatic growth and the reproductive products of mature fish), all ideally expressed in energy units. The remaining term, R_M, is the maximum ration defined in metabolic units (see Table 1, which also gives the coefficients used in calculating the power function relations between metabolism and body mass).

The procedure used is to solve equation 1 for an observed

TABLE 1. Parameter values applied to numerical estimates for herring, together with sources, dimensions and supplementary comments. Temperature conversions, as necessary, were made following Jones (1978).

Parameter	Usage and dimensions	Source and comments
$p = 0.8$	Assimilation coefficient (dimensionless)	Winberg (1956)
$m = 0.15$	Calorigenic coefficient (dimensionless)	Rounded to nearest 0.05 from Ware (1975)
$\alpha_S = 0.024$	Intercept of standard metabolism–body weight relationship ($kcal \cdot d^{-1}$) at 10°C (1 kcal = 4.184×10^3 J)	DeSilva and Tytler (1973). Converted to wet weight assuming dry/wet = 0.2
$\alpha_T = 0.120$	Intercept of maximum metabolism–body weight relationship ($kcal \cdot d^{-1}$) at 10°C	From DeSilva and Balbontin (1974) we derive 0.0995 for O-group herring on maximum rations. Rounded up to $5 \times \alpha_S$ to be consistent with active range from Holliday et al. (1964)
$\gamma = 0.8$	Power index of metabolism–body weight relationship	Mean of indices from DeSilva and Balbontin (1974) and DeSilva and Tytler (1973)
$R_M = 8.0T_S$	Maximum ration (multiples of standard metabolism)	Highest values ($\sim 17\% \cdot Wd^{-1}$) from DeSilva and Balbontin (1974). Assumes 1 g wet weight = 1 kcal

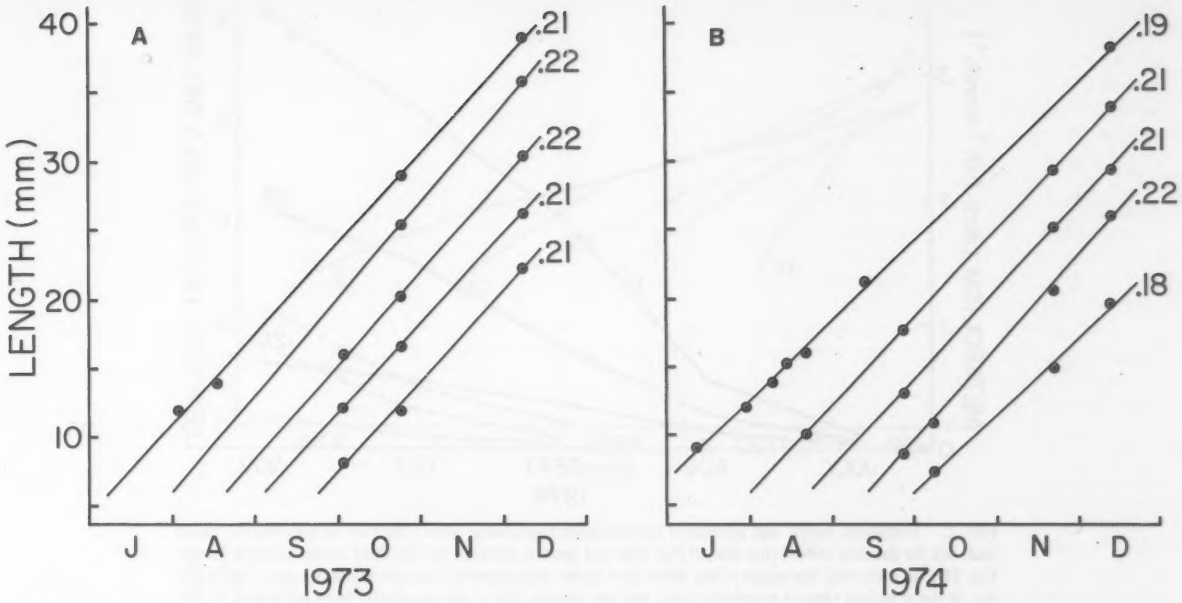

FIG. 1. Growth patterns observed by Lambert et al. (1982a) for the St. George's Bay larval herring that were selected for analysis here. Numbers to the right are estimated growth rates ($mm \cdot d^{-1}$) (A) 1973; (B) 1974.

ΔW, making adjustments necessary to the coefficients as they are affected by the temperatures observed in different seasons. Following Jones (1978), we assume an exponential effect of temperature on metabolism. The resulting estimate of R is then substituted in the mass balance equation, $pR = T + \Delta W$, yielding an estimate of T. The result is a balanced energy budget for a given body size and ambient temperature at a given time, which can be used for a variety of purposes. The application we make here is to compare the growth performances of O+ herring cohorts both within and between years.

St. George's Bay Herring

D. M. Ware, T. C. Lambert, and colleagues have conducted an extensive investigation of the fish production system of St. George's Bay, a large embayment of Northumberland Strait in the southern Gulf of St. Lawrence. Their data are suited to our analysis of herring bioenergetics.

Lambert et al. (1982a) described the growth patterns of successive cohorts of O+ herring that appeared in their samples at approximately 3-wk intervals in both 1973 and 1974. Figures 1A and 1B, adapted from their work, show the five most complete series from each year, which we use in the present analysis. The most obvious difference between years is that growth rates were relatively uniform in 1973 at 0.21–0.22 $mm \cdot d^{-1}$, while 1974 rates varied somewhat more widely, from 0.18 to 0.22 $mm \cdot d^{-1}$.

The same report (their fig. 14) also shows the median depths at which the young herring were captured as the season progressed. From Lambert et al. (1982b) we were able to associate water temperatures with the seasonally changing median larval depths during each of 1973 and 1974. The growth rates set out in Fig. 1 could therefore be compared with an index of average ambient temperature. To allow conversion from body length, given in the figures, to body mass (and energy content), T. C. Lambert (pers. comm.) kindly provided us with a length–weight distribution for St. George's Bay herring. That is, the basic inputs available for use were an index of ambient temperature and a size and calculated growth rate on a monthly basis for each of five cohorts of O+ herring in each of two years. For each cohort and year, we calculated energy budgets using equation 1 and the various parameters set out in Table 1.

A complete set of energy budgets permits a great many comparisons to be made including, for example, ration levels, growth efficiencies, and various metabolic components. We were interested that herring growth in both years, but especially in 1973, was relatively uniform for all larval groups, despite seasonal temperature decreases from roughly 18°C in July to 8°C in November. For this reason we present our analysis in terms of metabolic levels, which are directly affected by water temperature.

Fry (1947) introduced the concept of "metabolic scope for activity." By this he recognized that a basal (standard) metabolic level is required to sustain life, and that a maximum level cannot be exceeded on a sustained basis. Between the minimum and maximum constraints (its metabolic "scope") is a level at which the fish actually exists at a given time, which provides a measure of the proportion of scope that has been realized. Realizing scope is an index of the fish's capacity to mount activities such as growth.

Figure 2 provides, as examples, our estimates of the scope for activity and the realized metabolic level for each of two larval groups (the first and the third) for 1974 (see Fig. 1B). It is interesting to note in Fig. 2 that although the two observed growth rates did not differ greatly, the potential metabolic scopes and the proportions of scope actually realized both differ substantially. This is certainly a consequence of the different body sizes of larvae and the temperatures, but the empirical data used will also reflect the effects of other differences such as availability of suitable food. Despite the relative similarities

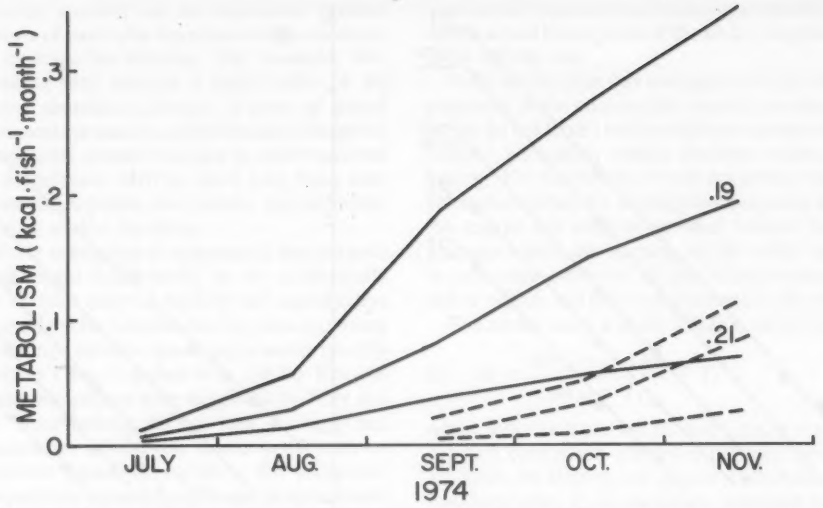

FIG. 2. Metabolic scope and estimated performance (metabolic niche) for two larval cohorts. Solid lines are for the first cohort (top line in Fig. 1B) and broken lines are for the third cohort (middle line in Fig. 1B). In each case the upper of the three lines is the maximum sustainable metabolic rate, the lower line is the standard (basal) metabolic rate, and the middle line is the metabolic level estimated by the model to have been actually realized by the larvae.

of the observed growth rate, it is clear from Fig. 2 that the two larval groups were living under quite different metabolic conditions.

Kerr (1980, and references therein) suggested generalizing Fry's "metabolic scope" concept to n dimensions of factors, depicting a "metabolic niche." In these terms, it is worth noting that the two short cohort histories of Fig. 2 provide an explicit picture of two such metabolic niches, each set in two dimensions (temperature and body size).

For ease of comparison among larval groups that differ in body size, it is convenient to generalize further from Fig. 2. If we normalize metabolic realization (i.e. the actual metabolic level) relative to the maximum sustainable level, in the form of plots of T/T_T, we lose information about absolute metabolic levels that differ because of body size differences but gain the ability to assess the effects of season that reflect temperature and, by implication, other confounded effects such as food availability. Plots of T/T_T, that is, of metabolic niche realization, are shown in Fig. 3A and 3B for the several herring cohorts observed in 1973 and 1974, respectively.

Inspection of Fig. 3A and 3B suggests two general conclusions. First, within years, the earliest cohort, detected in the net samples by mid-July, appears to be at a disadvantage over its total seasonal history. That is, in both years, despite its early start and consequently larger initial body size, the slope of the line of its metabolic realization remains lower than that of the succeeding larval cohorts. In both 1973 and 1974, later seasonal cohorts show a much more rapid rise in realization of their metabolic niche potential despite falling water temperatures from August on. The advantage of hatching early in the season, which presumably allows the larvae relative relief from the predator field by being larger and more active than succeeding cohorts, is perhaps overshadowed by lesser food availabilities, that is, it may have become too large to make effective use of the autumn zooplankton peak of abundance, which consists predominately of smaller organisms.

In support of the view that seasonally changing availability of suitable food may account for much of the residual variability not directly attributable to temperature and body size, Ware (1977) provides data on zooplankton availability during the autumn of 1974. His observations, which are based on vertical hauls using 80-μm mesh nets, show that zooplankton abundance was high over the period October through December, peaking in November. While the mean particle size in the zooplankton increased steadily over that period, it remained small, averaging from 400 μm in October to 800 μm in December. Thus, Ware's observations suggest that both the abundance and suitability of prey increased during the period that the newer herring cohorts were showing increased metabolic realization despite falling water temperatures. Lambert et al. (1982a) provided empirical relations showing the association of zooplankton size and abundance with larval size. In addition, T. C. Lambert (pers. comm.) has pointed out that herring larvae probably suffer maximum competition for food in midsummer when he finds quantities of larvae of other species, notably white hake and mackerel, present in the samples. These species are much faster growing than herring and tend to move out of the Bay by October, leaving the field to the herring.

The second generalization supported by Fig. 3A and 3B is that 1973 was a generally better year for metabolic realization by the several larval cohorts than was 1974. This is reflected in the generally higher metabolic levels achieved by the 1973 cohorts, including the first cohort which, although characteristically less ebullient than succeeding groups, nevertheless fared substantially better than the comparable cohort of 1974. Neither temperature nor body size seems to have been remarkably different during the two years. Unfortunately, data on zooplankton abundance are not available for 1973, so that we cannot

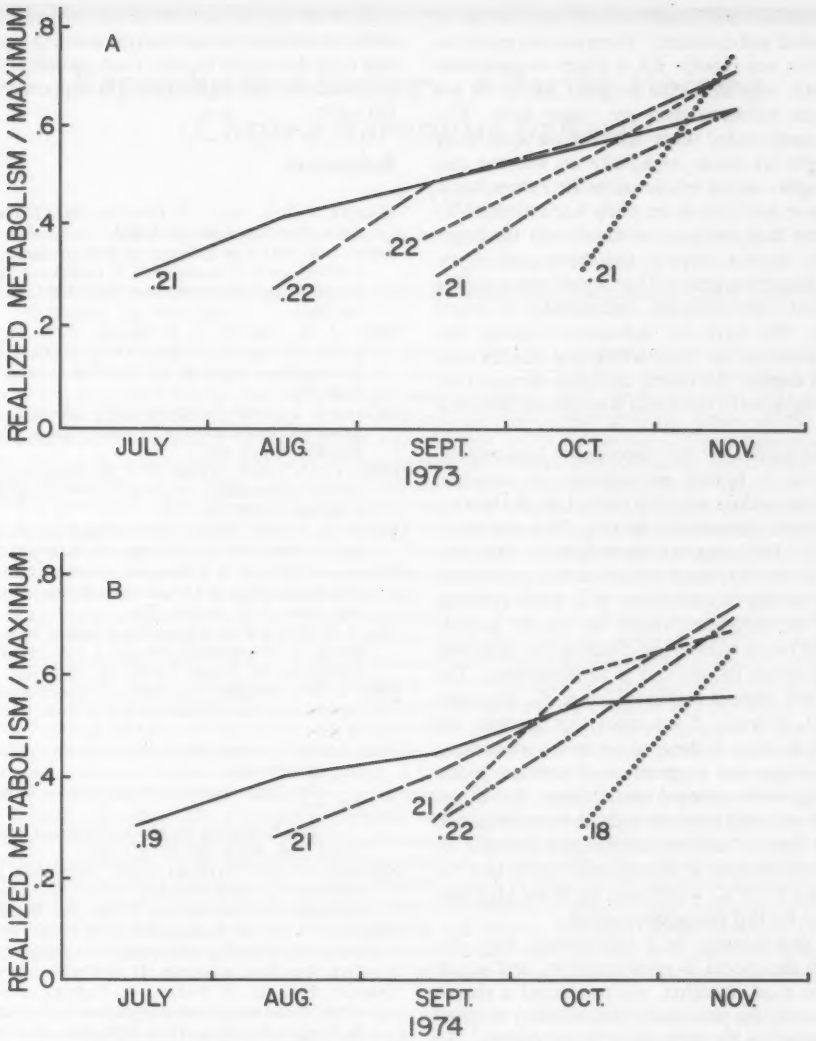

FIG. 3. Proportion of metabolic scope (niche) realized by five larval cohorts in relation to season. (A) 1973; (B) 1974.

verify that the higher metabolic levels mean that feeding conditions for the herring were better in 1973 than in 1974.

Discussion

The application of even this relatively simple type of bioenergetics model to herring seems to verify the general expectation that analysis of underlying bioenergetics reveals features of production systems not revealed by observations of the resultant growths of cohorts. The specific conclusion that emerges here, because of the uniquely exemplary field observations of D. M. Ware, T. C. Lambert, and their colleagues, is that herring cohorts are occupying quite different metabolic niches during the spawning and growing season, although the resultant growth appears quite uniform. Apparently the advantages of early spawning, resulting in early attainment of relatively larger body size, are offset by superior feeding conditions of the late season resulting in much more rapid increases in realization of their metabolic potential by later cohorts, despite the rapidly falling ambient temperatures that they experience.

These conclusions are subject to severe limitations because of the paucity of both sampling and reliable physiological bioenergetics information for clupeoids in general or herring in particular. For example, in this particular analysis, we have been careful to restrict comparisons to succeeding cohorts of successive year-classes of a single species, but important uncertainties remain in calibration of our example within the model. Sampling error, due to net avoidance, for example, is an ubiquitous problem in larval fish analyses: we do not know whether such problems might have affected the accuracy of the size and growth analysis offered here, but biasses could be

present that would affect the clarity with which the larval cohorts can be identified and measured. There are also precision errors that may affect our results: for a given measurement system (i.e. a ruler), smaller sizes (lengths) of larvae are measured to a lesser precision than are larger sizes. This problem becomes compounded when conversions from body length to body weight are made, especially, as was the case here, when body length–weight relationships are extrapolated. Quite simply, we have less faith in the body size estimates we used for small larvae than we have in those used for larger larvae. Additionally, there is scope in the above analysis for error introduced by something akin to a Lee's phenomenon. The larval stanzas sampled were subjected, undoubtedly, to severe predation mortality. We have no indication whether this mortality was size-selective, or, if so, which size stanzas were affected and to what degree. We merely accepted the observed larval sizes as representative of the actual populations present at a given time.

Calibration of the model by the appropriate bioenergetic parameters gives rise to further uncertainties of uncertain dimensions. The various values set out in Table 1 are the best we can make of the available literature for herring. They are not all that we would wish for. With respect to the authorities cited, and the many others we do not cite, much remains to be explored and verified concerning herring bioenergetics. It is worth pointing out, however, that the parameter values we list do provide plausible results. Our major reservation concerns the estimated values for R_M (maximum ration) and p (assimilation). The literature suggests, not without ambiguity, that R_M decreases with body size (W), whereas p increases (for herring, not necessarily for other species). If these suppositions are correct, which is far from certain, our supposition of constant p and variable R_M (varying with standard metabolism, T_S) is not supported. Further work could confirm or refute our premises. It is also worth noting that we have no experimental grounds for use of the exponential method of temperature correction for herring over the range 8–18°C, which may be in the high part of the tolerable range for this temperate species.

As a means of determining, in a preliminary way, the parameters to which the model is most sensitive, and which therefore require the most attention, we conducted a simple sensitivity analysis using the procedures described by Kitchell et al. (1977). Allowing for the differences in the models, our results were strikingly similar to those obtained by Kitchell et al. (1977) and to a similar analysis conducted by Majkowski and Waiwood (1981), both in terms of which parameters were sensitive and the relative magnitudes of estimated sensitivity. In general, the most sensitive parameters are those associated with ingestion (p, R_M) and with the metabolic level (α_S, α_T). The remaining parameters were either linear, in the sense that a 10% change in parameter value caused an equal change in the estimated T, or caused lesser effects. Clearly, the accuracy of the results we present here depends most critically on the estimates of p, R_M, α_S, and α_T, and these need to be further studied in laboratory and field energy balance experiments.

Effort to refine these parameter estimates will prove worthwhile. The ability to prosecute bioenergetic analyses of herring production systems, as with other marine production systems, will shed new and different light upon the fisheries production process in marine environments. In particular, the attendant ability to separate factors such as ambient temperature and body size from the related factors, food availability, for example, that affect marine fish production will support analyses of substantial utility.

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Reproductive Biology of Pacific Herring (*Clupea harengus pallasi*)[1]

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Hay, D. E. 1985. Reproductive biology of Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 42 (Suppl. 1): 111–126.

Most British Columbia herring begin sexual maturation in the late summer and become sexually mature in the subsequent March or April. As they mature, most stocks migrate from summer feeding grounds to overwintering areas and then to shallow nearshore spawning areas. Also, newly recruited, sexually maturing fish join the adult spawning stocks, either on the summer or winter grounds. These events occur in an unpredictable environment. Consequently, reproduction in Pacific herring (*Clupea harengus pallasi*) may be viewed as a biological problem of maintaining synchrony and precision: specifically the synchronous maturation of (1) males and females and (2) the recruit spawners with the adult fish that have spawned in previous years. Biological precision is required to ensure that gametes are released at the correct place at the correct time. Further precision is required to achieve an appropriate balance between egg number and egg size, and then to control the density of eggs deposited on the bottom. The annual temperature regime is a vital regulator of these processes. Generally, the warmer the temperature, or lower the latitude, the earlier the maturation and spawning time. There are some notable exceptions that indicate local adaptation to other environmental cues. Also, experimental work indicates that food supply can affect the maturation rate. Intensities of egg depositions are generally similar among Pacific North American stocks, and indeed for many documented herring spawnings from Asian and European stocks. It has been shown that eggs in the middle of very thick spawns have lower survival so there is a selective advantage for biological mechanisms that ensure more even and lighter egg densities. This paper suggests that egg density in Pacific herring is controlled by a biological feedback mechanism involving milt concentration and hydrographic factors. Earlier spawners tend to be larger and there is a positive relationship between female size and egg size, a tendency consistent with other herring stocks and species. Size-adjusted fecundity, when compared among different regions and years, is strikingly uniform within British Columbia. On a broad geographic scale (California to Alaska), size-specific fecundity declines with latitude. Recent experimental work reveals that total egg number is higher at early stages of maturation and decreases as spawning time approaches. Presumably, this decrease reflects selective resorption of some developing oocytes, and probably occurs in response to available body energy. The duration and geographical variation in spawning time is relevant to questions concerning the evolutionary and taxonomic relationships between Pacific herring and Atlantic herring (*Clupea harengus harengus*). Other aspects of reproductive biology have important management implications, particularly for (1) predicting recruitment, (2) deriving stock estimates from spawn surveys, and (3) managing fisheries.

La plupart des harengs de la Colombie-Britannique commence leur maturation sexuelle à la fin de l'été et deviennent sexuellement matures en mars ou en avril de l'année suivante. Au cours de la maturation, la plupart des stocks migrent des zones d'alimentation estivales vers les habitats hivernaux pour ensuite se diriger vers les frayères côtières peu profondes. De plus, les nouvelles recrues en voie de maturation se joignent aux stocks d'adultes reproducteurs, soit dans les aires d'été ou dans les quartiers d'hiver. Ces évènements se produisent dans un environnement imprévisible ; par conséquent, on peut envisager la reproduction du hareng du Pacifique (*Clupa harengus pallasi*) comme un problème biologique pour ce qui est du maintien du synchronisme et de la précision, plus précisément la maturation synchronisée (1) des mâles et des femelles et (2) des nouveaux géniteurs et des adultes qui ont frayé les années précédentes. La précision biologique est nécessaire pour que les gamètes soient relâchées au bon endroit, au bon moment. Une précision additionnelle est aussi requise pour qu'il y ait un équilibre approprié entre le nombre et la taille des œufs, puis un contrôle de la densité des œufs déposés sur la fond. Le régime thermique annuel est un régulateur vital de ces processus. En général, plus la température est élevée, ou plus la latitude est basse, plus tôt la maturation et la fraie ont lieu. Il existe des exceptions remarquables qui portent à croire à des adaptations locales à d'autres stimuli environnementaux. Des travaux expérimentaux ont en outre révélé une incidence de la quantité de nourriture sur le taux de maturation. L'intensité de la ponte d'œufs est généralement semblable parmi les stocks du Pacifique nord-américain et, en fait, pour un grand nombre de fraies observées dans les stocks de hareng en Asie et en Europe. Il a été prouvé que les œufs au centre de frais très épais ont un taux inférieur de survie ; des mécanismes biologiques confèrent donc des avantages sélectifs qui assurent des densités plus égales et moins concentrées des œufs. La présente étude suggère que la densité des œufs du hareng du Pacifique est contrôlée par un mécanisme de contre-

[1]This paper was presented at the International Symposium on the Biological Characteristics of Herring and Their Implication for Management, convened at Nanaimo, B.C., June 20–22, 1983, commemorating the 75th anniversary of the Pacific Biological Station.

réaction biologique qui fait intervenir la concentration de la laitance et certains facteurs hydrographiques. Les géniteurs qui frayent tôt sont souvent plus gros ; il existe aussi une relation positive entre la taille de la femelle et des œufs, tendance qui se retrouve dans d'autres stocks et chez d'autres espèces de hareng. La fécondité ajustée en fonction de la taille, comparée entre régions et années, est extraordinairement uniforme à l'intérieur de la Colombie-Britannique. Sur une vaste échelle géographique (de la Californie à l'Alaska), la fécondité en fonction de la taille baisse selon la latitude. Selon de récents travaux expérimentaux, le nombre total d'œufs est plus élevé aux premiers stades de maturation et décroît quand la fraie approche. Il y a lieu de croire que cette baisse reflète une résorption sélective de certains oocytes en développement laquelle se produit probablement en réaction à l'énergie corporelle disponible. La durée et la variation géographique du temps de fraie sont significatives par rapport aux questions touchant les relations évolutionnaires et taxonomiques entre les harengs du Pacifique et de l'Atlantique (*Clupea harengus harengus*). D'autres aspects de la reproduction ont d'importantes conséquences gestionnelles, en particulier pour (1) la prédiction du recrutement, (2) la dérivation d'estimations des stocks à partir d'études sur le frai et (3) la gestion des pêches.

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Every year, Pacific herring (*Clupea harengus pallasi*) spawn along approximately 500 km of the British Columbia coastline. The total annual spawn deposition consists of 300–500 individual spawnings. These are distributed among a number of different general spawning locations, such as large bays or inlets. General spawning locations are roughly the same from year to year but within a general location, the precise site may change between years. For instance, of the 26 000 km of the British Columbia coastline (Statistics Canada 1978), about 12% or 3100 km have been documented as spawning sites (Haegele and Fitzpatrick 1983). For the British Columbia coast at large, most spawning occurs during March and April, but with specific locations, spawning time is more exact (±10 d). This specificity of spawn timing and spawn sites is remarkable in view of herring migratory habits. Generally, summer months are spent on offshore feeding grounds. Then in the late fall or early winter many stocks move to overwintering areas. This pattern is documented for most Pacific herring populations from California (Miller and Schmidtke 1956), British Columbia (Taylor 1964), southern Alaska (Rounsefell 1930), the Bering Sea (Barton and Wespestad 1980), Kamchatka (Svetovidov 1952), the Sea of Okhotsk (Tyurnin 1973), and the Sea of Japan (Motoda and Hirano 1963). The timing of these migrations varies considerably among populations. From the overwintering areas they travel to spawning areas. Recruit spawners join the adult stocks during the maturation process. This can be a significant event because in some years recruits make up the majority of the total spawning stock (Tester 1955).

The coordination of these movements with the processes of maturation and spawning is a biological problem requiring precision and synchrony. Prior to the spawning act a variety of behavioral, physiological, and ecological processes must operate to control (1) the temporal rate of maturation, (2) the precise location of spawning grounds, (3) the timing of spawning, and (4) the synchrony of readiness between the sexes. Additional controls operate during the spawning act to control the deposition of the adhesive demersal eggs and the duration of the spawning act.

This paper presents previously unpublished material and reviews other work relevant to herring reproduction. The analysis begins with the early oocyte maturation process in the late summer. This is followed by description and analyses of factors controlling egg size and number, spawning time, and demographic and geographic variation in spawning. The paper concludes with a discussion of the relevance of research in reproductive biology to management of Pacific herring.

Maturation

Oocyte Development

The gonads of most British Columbia stocks, when examined during the early summer, resemble those of immature fish: testes and ovaries are long, thin, and inconspicuous in the body cavity. During the fall months the gonads of both sexes begin to grow rapidly and growth levels off as the spawning season approaches (Hay and Outram 1981). When annual gonad growth is expressed as a percentage of total body weight (or as the gonosomatic index, GSI) several developmental trends appear: testes growth in males precedes ovary growth in females, and males mature earlier than females (Fig. 1). Samples used for this analysis were taken about 20–30 km south of Nanaimo, B.C., an area where herring usually spawn in mid-March. The maximal GSI for testes was reached in late January and early February. In contrast, the GSI for ovaries continued to increase until spawning. The decrease in mean GSI for both sexes in March reflects the inclusion of spent and partialy spent fish. This difference in maturation rate between the sexes is similar to Atlantic herring (*Clupea harengus harengus*) (Blaxter and Holliday 1963).

Throughout the year, the GSI increases more rapidly in larger females than in smaller females (Fig. 2) and the ultimate GSI in large females is higher than the GSI of smaller females (Fig. 3). Large females, defined here as those over 22 cm, reach a maximum GSI of about 30, whereas the GSI of small fish is usually in the 20's. As a measure of maturation, the GSI is superior to the Hjort scale or its modified version (Hay and Outram 1981) sometimes used for Pacific herring (Table 1). It is less arbitrary and easily quantified. On the other hand, the GSI is often not a practical assessment for shipboard work because accurate weighing is required. Also, a simple GSI might not reveal some of the obvious early gonad development that can be seen (i.e. stage III versus II in Table 1) by eye but that is not sufficient to increase the gonad weight or GSI.

Temporal Changes in Oocytes

Maturing female herring have two groups of immature eggs or oocytes in their ovaries: larger maturing oocytes and smaller

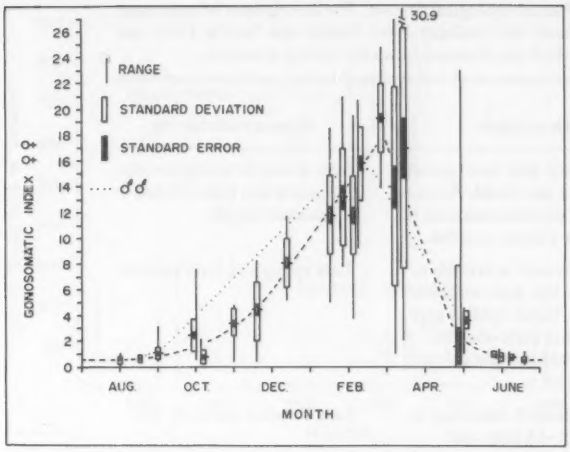


FIG. 1. Seasonal changes in the GSI from a nonmigrating stock of herring in the southern Strait of Georgia, B.C. Means, standard deviations, and standard errors are shown only for females. The development of the male GSI is indicated by the dotted line.

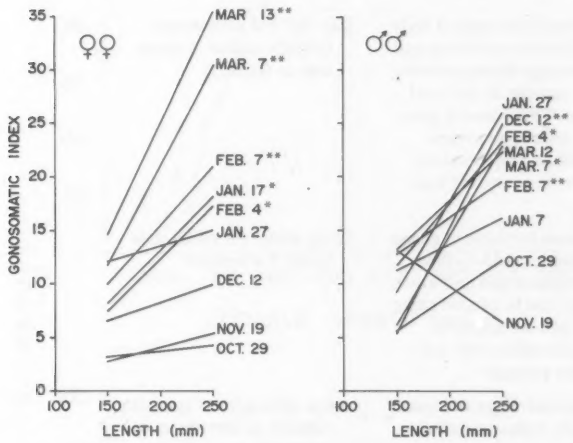
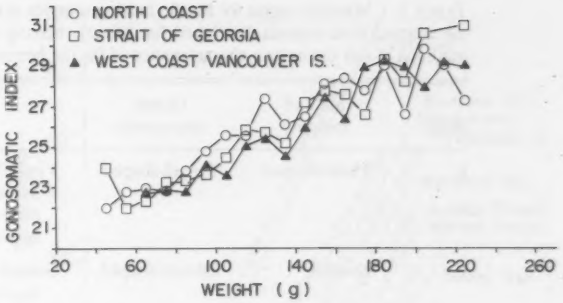


FIG. 2. Seasonal change in the size-specific GSI of males and females (adapted from Hay and Outram 1981). Statistically significant correlation coefficients at the 0.05 and 0.01 probability levels are indicated by single and double asterisks, respectively.

resting oocytes that will develop in the future. Immature herring have only resting oocytes (Bowers and Holliday 1961). Similar oocyte development occurs in British Columbia herring (Fig. 1). Ovaries from samples collected throughout the year were analysed histologically and diameters were measured for each of the two size groups (Fig. 4). In July and August, resting and maturing oocytes could not be distinguished by size. Beginning in September, there was clear separation of the size groups. Subsequently, the developing oocytes rapidly increased in diameter to a mean of about 700 μm in March. The maximum size of the resting ovaries was approximately 150 μm. Therefore, the presence of oocytes with diameters greater than 150 μm is indicative of a maturing female. These size ranges were confirmed in a later study of egg development from offshore samples taken in September and November. On each date, 50 measurements of oocyte diameters were made from his-



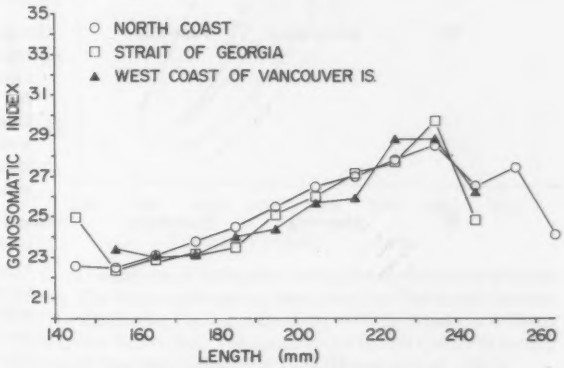


FIG. 3. Comparison of GSI among females of different weight (upper panel) and length (lower panel). Small herring have a mean GSI of about 20. The number of females greater than 230 mm was small and the decrease in GSI in large females could be sampling error. The data were collected in 1980.

tological sections of ovaries from about 35 females. There were two approximate size-classes in the September sample: a small group with diameters less than 150 μm (the resting oocytes) and a larger group with diameters between 200 and 500 μm (the maturing oocytes). In November 1980, the size distribution of the resting oocytes was unchanged, but the maturing oocytes had grown and ranged from about 300 to 700 μm. Therefore, the presence of oocytes larger than 150 μm (diameter) is a satisfactory criterion for distinguishing between maturing and immature females.

A Maturity Ogive Based on Egg Diameters

Some analysts of the British Columbia herring fishery have postulated that age- or size-specific maturation schedule might change among years, perhaps associated with changing stock densities, growth patterns, or other biotic or abiotic factors (Walters 1982, Pearse Commission analyses). The specific suggestion which was contrary to previous understanding (Taylor 1964), was that substantial proportions of age 3 and 4 fish might remain immature and recruit at age 5 or later. This suggestion was tested in the fall of 1982 when samples taken in the central and northern areas of British Columbia were analysed histologicaly and maximum oocyte diameters were measured for approximately 1000 females. The a priori hypothesis was that most females of age 3 and greater were maturing. To be deliberately conservative, all eggs less than 170 μm (compared

TABLE 1. Maturity stages for Pacific herring samples at the Pacific Biological Station. The descriptions of each stage are adapted from criteria developed for Atlantic herring (Bowers and Holliday 1961; Parrish and Saville 1965) and modified to suit the unique characteristics of Pacific herring, which are exclusively winter–spring spawners.

Stage	State of maturity	Gonad appearance	Description	Approximate timing
I.	Undeveloped	Thread-shaped	Virgin herring with small gonads, less than 2 mm broad. Accurate macroscopic determination of sex in not usually possible	Year-round for young herring, usually less than 150 mm in standard length
II.	Starting	Ribbon-shaped	Gonads increased in breadth to 3–5 mm. Sex determination possible. Testes reddish grey colored and knife-shaped; ovaries reddish wine colored and rounder	Late spring and early summer
III.	Developing	Tube-like	Gonads thickened, increased in breadth (5–15 mm) and elongated, but do not extend full length of body cavity. Ovaries red to reddish orange with granular appearance; testes reddish grey with smooth texture	Late summer and early fall
IV.	Maturing	Prominent	Gonads extend full length of body cavity. Ovaries reddish orange to yellow; eggs distinguishable, opaque, variable in size, and separable. Testes mostly grey and will ooze sperm when sliced. Blood vessels clearly visible in the ovary and testis walls	Late fall and early winter (slightly earlier in males than in females)
V.	Mature	Bulging	No blood vessels visible in gonad walls. Ovaries gold–yellow; eggs transparent and uniform in size. Eggs can be exuded under pressure and are adhesive. Testes milk-white; milt will flow under pressure	Early winter for males, late winter for females
VI.	Ripe	Running	Eggs transparent. Eggs and sperm flow easily without external pressure	A few days prior to spawning (usually in late winter or early spring)
VII.	Spent	Baggy	Gonads slack. Ovaries may contain a few residual eggs. Testes limp and bloodshot	Early spring for the first few weeks following spawning
VIII.	Recovering	Compressed	Gonads wine-colored and usually longer and thicker than in stage II. Blood vessels prominent. This stage passes into stage III, but may resemble stage II in the process	Late spring and early summer

with the 150 μm criterion mentioned earlier) were classified as immature or as resting oocytes; larger oocytes were classified as maturing and a female with oocytes exceeding 170 μm diameter was judged as maturing. The resulting maturation ogive indicates that nearly all 3-yr-old and older herring were maturing, and that a substantial proportion of age 2 females were also maturing (Fig. 5). Similar maturity ogives were obtained in 1983 in several areas of the coast.

This length-specific maturation schedule is typical of the trend described for most Pacific herring, but age-specific maturation varies with latitude. At the southern extremes of their range, in California and the Yellow Sea, most herring mature at age 2 (Spratt 1981; Cheng 1980). Maturation begins later, at age 4 or 5, in the northern Asian and Alaskan stocks (Barton and Wespestad 1980).

Egg Size and Number

Recent experimental studies indicate that egg number in Pacific herring is determined late during maturation, perhaps as

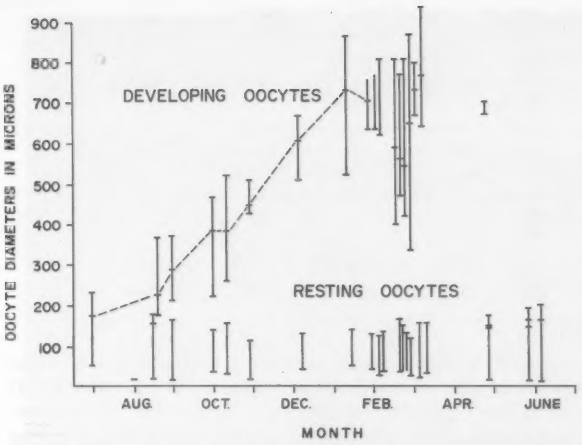


FIG. 4. Oocyte sizes and development throughout the year. Size ranges shown represent egg diameters present at the time of measurement. The broken line joins mean diameter of the developing oocytes.

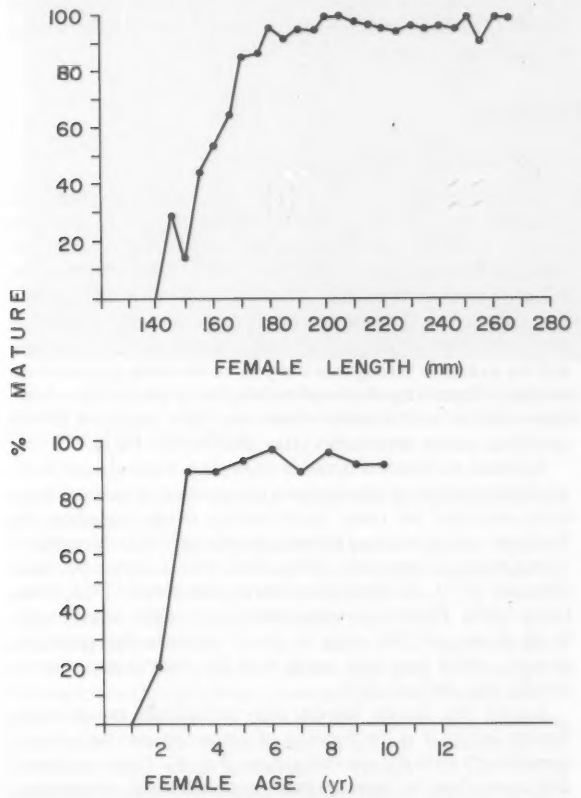


FIG. 5. A maturity ogive based on oocyte diameters. For each female examined, 10 of the largest oocytes observed were measured.

late as 20–30 d prior to full sexual ripeness (D. Hay and J. Brett, unpubl. data). During the early stages of development, females begin to develop more eggs than they bring to full maturation. During maturation, the egg number decreases, probably through a selective resorption of maturing oocytes. Experimental impoundment studies compared fed and unfed females. Feeding

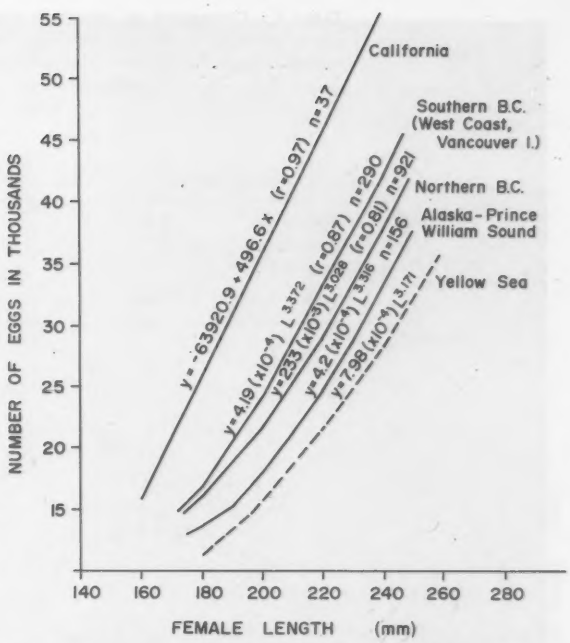


FIG. 6. Comparison of fecundities among Pacific herring at different latitudes. The linear regression equations are from Rabin and Barnhart (1977) for California, Paulson and Smith (1977) for Alaska, and Cheng (1980) for the Yellow Sea. The equations for British Columbia herring are adapted from data collected in 1974 (Hourston et al. 1981).

resulted in a general increase in mean length and weight, total body size, with a corresponding increase in gonad weight, but there was little effect on egg size (D. Hay and J. Brett, unpubl. data). The significance of this is that herring may increase both their somatic and gonadal biomass during favorable feeding conditions but egg size is relatively constant when compared among females of similar length. Egg size, however, varies with female size: larger females have larger eggs (Kingston 1983).

Along the Pacific coast of North America the total size-specific fecundity is inversely related to latitude. California fish have more eggs than British Columbia herring, which have fewer than Alaskan herring. This trend was described by Paulson and Smith (1977). In the present paper, I use additional California data (Rabin and Barnhart 1977) and British Columbia data to examine this trend (Fig. 6). Rabin and Barnhart (1977) included estimates both of total ovary weight and fecundity. This permits an estimation of egg weight for California herring (ovary weight divided by egg number). When calculated this way it appears that California fish have slightly smaller eggs than British Columbia herring (Fig. 7). There is, however, considerable variation about these regression lines and the size-adjusted differences in egg weight between California and British Columbia are slight, whereas the differences in fecundity are substantial. The GSI estimates of California herring (calculated as a mean of 24.5 from data of Rabin and Barnhart) are roughly the same as those in British Columbia (Fig. 2 and 3). Therefore, if the GSI is approximately the same, and egg weights are only slightly different, then the likely explanation for the greater size-specific fecundities of California herring is that they have a steeper length–weight relationship. A cursory

TABLE 2. Comparison of relative fecundities (eggs per gram of total body weight) among different locations and between years for British Columbia. The California sample was collected in 1975 and the data were published in Rabin and Barnhart (1977).

	1974				1980			
	Mean length	*n*	eggs/g	SD	Mean length	*n*	eggs/g	SD
North Coast	218.9	1715	204.0	40.4	184.5	921	186.8	33.3
West Coast	217.5	855	217.1	34.2	191.6	290	197.2	31.5
Strait of Georgia	224.5	723	224.5	16.9	191.1	431	205.2	53.5
California, 1975	184.6	37	216.2	20.7				

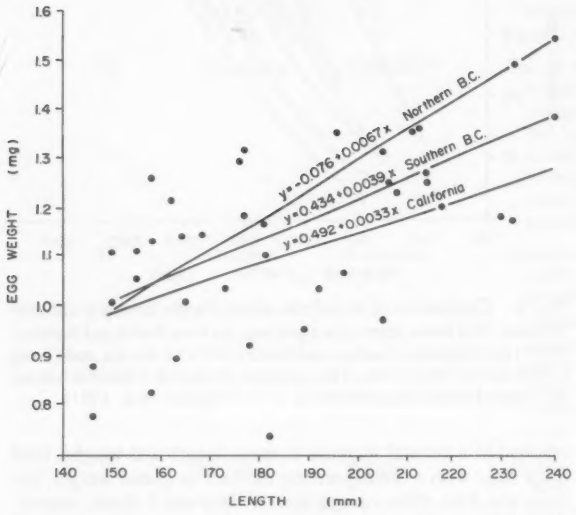


FIG. 7. Comparison of egg sizes between California and British Columbia. The female length–egg weight regression for California herring was calculated from data presented by Rabin and Barnhart (1977). The British Columbia data were collected in 1980. The points, shown for individual California fish, illustrate the variation in these data.

comparison of length–weight data from different latitudes suggests that for a given length, herring tend to be heavier in the south, but there may be problems with the comparison of length–weight data collected by different investigators on different stocks varying in their degree of maturation. Resolution of such problems is beyond the scope of this paper.

The number of eggs per gram of total body weight is a useful measure of relative fecundity, particularly for spawn surveys used to estimate total biomass of spawning fish. The advantage of the eggs per gram estimate in Pacific herring is its relative uniformity over size and geographical regions. For instance, in herring, egg number increases exponentially with female length. Egg size also increases with fish size. Hempel and Blaxter (1967) found that egg weights of recruit spawners were significantly less than those of larger, older repeat spawners. Consequently, the number of eggs per unit weight is more similar among size groups (Table 2) than is total fecundity. However, the eggs per gram estimate does vary slightly with female size. This accounts for the differences in the relative fecundity estimates for data collected in 1974 and 1980 (Table 2). During 1980 most of the samples were collected later in the spawning season and consisted mainly of smaller fish. As a rule of thumb for British Columbia herring, an estimate of 200 eggs/female gram is used (Hay and Fulton 1983). This represents a total of 10^8 eggs deposited per tonne of spawning herring of both sexes and is convenient for making approximate estimates of the tonnages of spawning fish from spawn surveys. Geographic differences in relative fecundity seem small. The California sample had a mean length of 184.6 mm and a relative fecundity of about 220 eggs/g (calculated from data presented by Rabin and Barnhart 1977).

Spawning

Winter and Prespawning Aggregations

Winter aggregations form in several areas on the British Columbia coast. One location in the Gulf Islands in southern Georgia Strait was often the site of a major winter fishery for meal production in the 1950's and 1960's. The fish remain in this and other winter areas for several months while their gonads ripen. In British Columbia there appear to be some nonmigratory herring that do not go to offshore summer feeding grounds and are available throughout the year in the same approximate location. These migratory and nonmigratory groups can sometimes coexist in the same waters and later segregate as the spawning season approaches (Hay and Outram 1981).

Seasonal movements between spawning, feeding, and overwintering grounds or similar types of consistent migrations have been described for many local herring stocks including the Hokkaido spring herring (Motoda and Hirano 1963), Norwegian spring herring (Dragesund 1980), Gulf of St. Lawrence herring (Messieh 1975), and Bering Sea herring (Shaboneev 1965; Prokhorov 1968). Prior to spawning these large winter assemblages break down and fish seem to travel closer to the spawning grounds where they may again hold for short times prior to moving into shallow areas.

Among the lesser known and understood prespawning herring behavior is the forming of dense fast-moving schools immediately over the spawning areas (Fig. 8). Large groups of fish come close to shore swimming quickly and, apparently, randomly. At times these "prespawning" congregations are so dense that the fish seem to push themselves out of the water. Herring appear particularly vulnerable to predation by sea birds at this time, and herring schools can often be located by the presence of dense flocks of birds. Similar prespawning behavior has been described for Departure Bay (Munro and Clemens 1931). Tyurnin (1973) has described prespawning Okhotsk herring, when seen from the air, as "ribbons — often tens of kilometers in length." Perhaps herring use these shallow-water

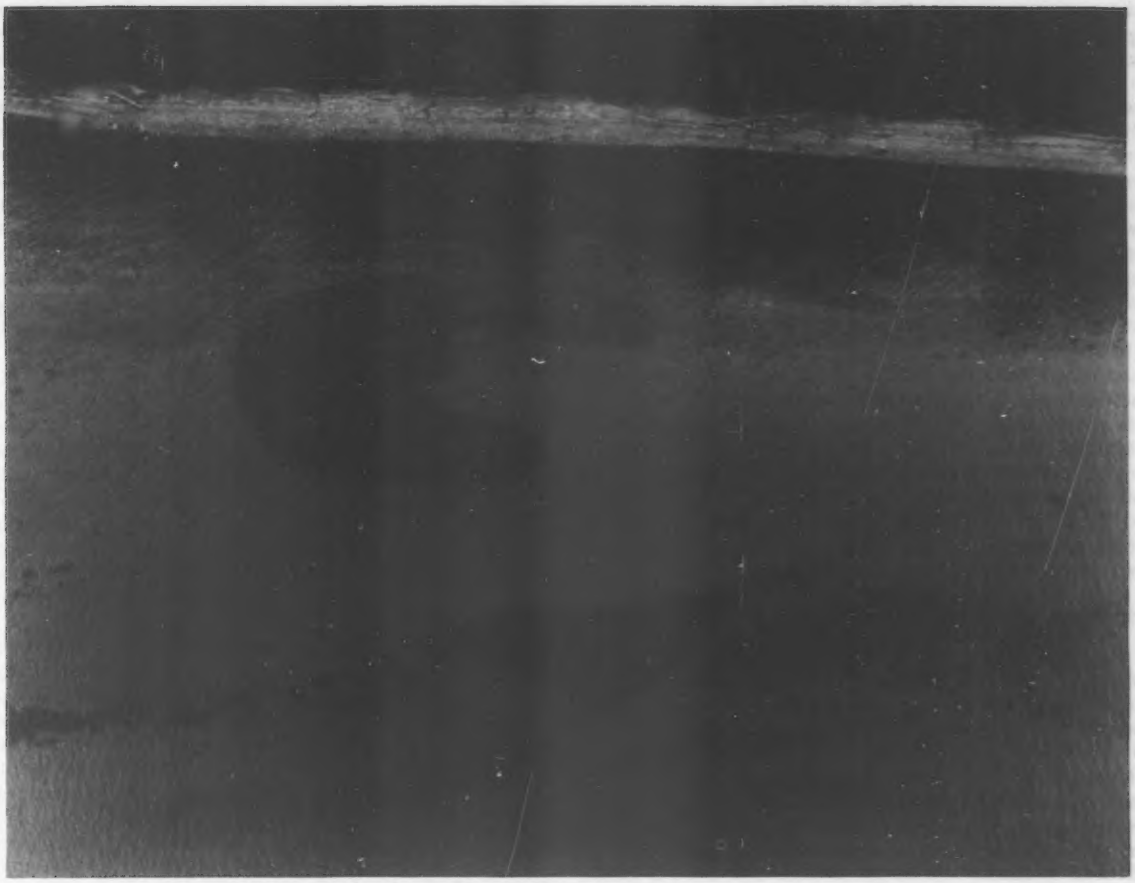


FIG. 8. Aerial photograph of herring schools on the spawning grounds 5 d before the start of spawning. The dark semicircular and triangular patches are dense, rapidly moving herring schools of 20–50 m width. The darker colour at the top of the photograph is shallow submerged vegetation at the water's edge.

excursions to sample the local water and substrate conditions prior to spawning.

Although our understanding of the precise factors initiating spawning is poor, we do know that herring spawnings are restricted by depth, temperature, substrate type, and possibly other factors, such as high sediment loads either in the water column or on the bottom. Iles and Caddy (1972) suggested that a combination of hydrographic and topographic features guide herring to the Georges Bank spawning grounds. Tyurnin (1973) noted drastic changes in the Okhotsk Sea herring spawning distribution, which he attributed to annual variation in ice conditions and water temperature. Fontaine et al. (1978) attributed changes in spawn distribution of Atlantic herring spawning off the west coast of France to changes in water chemistry, specifically a general decrease in the amino acid concentration although they found an increase in serine concentration, a substance known to act as a repellent for salmonids. Barton and Wespestad (1980) stated that time of spawning in Bering Sea herring, usually between late April and late May, is associated with weather conditions, particularly the ice breakup. Tyurnin (1973) made a similar observation on the spawning time of the Sea of Okhotsk herring.

Spawning Behavior

The earliest sign of spawning is the presence of milt in the water. Usually the concentration is sufficient to result in a striking discoloration turning the water white. Sometimes, at the early stages of a major spawning, I have observed small patches of milt-discolored water, less than a hectare, but with no egg deposition. Also, in a March 1982 field study in Barkley Sound, on the west coast of Vancouver Island, we took small beach seine samples on the spawning grounds as the fish were spawning. During subsequent analyses, we noticed that almost all of the males were totally spent, but most females were only partially spent. These observations suggest that males probably initiate the spawning act followed by females depositing eggs on the substrate.

It is essential that males and females are in reproductive synchrony to ensure fertilization. The process of releasing small quantities of milt would ensure that the ultimate release of gametes from each sex was not completely wasted. This explanation, however, does not address the question of the motivation or selective advantage of the males, which take a risk and release their gametes first. Perhaps if such early starts

did precipitate a major spawning then those males with their gametes first in the water would almost certainly stand a better chance of fertilizing more eggs than later spawning males.

Detailed behavioral analyses of captive herring spawning were described by Hourston et al. (1977) and Stacey and Hourston (1982). They described several discrete behavior patterns including *substrate testing* and *substrate spawning*, both of which involve contact between the urogenital papilla and the substrate. Their observations seem generally consistent with those in the natural environment (Rounsefell 1930). The major differences concern (1) the clarity of the water and (2) the substrate available for egg deposition.For instance, the milt concentration in most natural spawning results in negligible visibility. Also, many spawnings occur at night in darkness (Miller and Schmidtke 1956). It is difficult, therefore, to understand how visual stimuli can operate once the spawning act has begun. In addition, not all eggs are released directly on the substrate. In very heavy spawnings the number of egg layers deposited increases so that most eggs are deposited on other eggs. The significance of this is that if females were to use tactile sensory information to assess the substrate, the only surface available would be that of previously deposited eggs. Also, there is evidence from captive fish studies that some eggs may be released in midwater (Stacey and Hourston 1982).

Spawn Deposition and Egg Density

Each year during the spawning season, local fishery officers along the British Columbia coast take detailed records on the precise location, timing, physical dimensions, and intensity of spawnings (e.g. Hourston and Haist 1981; Chalmers and Sprout 1981). These records have been taken for over 30 yr and form the basis of annual escapement estimates or an estimate of fish not captured by the preceding fishery. They also provide an opportunity to compare annual spawning patterns (intensity, magnitude) and timing and among year, within, and among different locations.

For each spawning, the intensity of egg deposition, or the number of layers of eggs, is judged by Fishery Officers as one of several categories (Table 3). This categorization is a matter of judgement that is bound to vary among officers. However, we now have records of about 18 000 spawnings along the British Columbia coast from 1928 to 1982. From this massive series of records certain geographical and temporal trends emerge that are extremely consistent and are therefore real phenomena and not artifacts of arbitrary or inconsistent evaluation.

TABLE 3. Classifications of egg intensities, as recorded during British Columbia spawn surveys. The suggested number of eggs corresponding to each classification is a rough approximation. (Adapted from Chalmers and Sprout 1981)

Intensity classification	Estimated number of eggs/m^2	Weighting factor
1. Very light	50 000	0.05
2. Very light to light	180 000	0.20
3. Light	420 000	0.40
4. Light to medium	665 000	0.65
5. Medium	1 008 000	1.00
6. Medium to heavy	1 417 000	1.40
7. Heavy	1 889 000	1.90
8. Heavy to very heavy	2 423 000	2.40
9. Very heavy	3 019 000	3.00

There are some consistent differences in intensity among geographical areas. Naden Harbour in the northern Queen Charlotte Islands and Ganges Harbour in Saltspring Island in the southern Strait of Georgia each have the lightest intensities and are the earliest of British Columbia spawnings. Light spawning intensity is also common among very late spawnings. Therefore, perhaps the mean intensity and mean time of spawn vary together. Egg intensity varies also with lengths of individual spawnings: shorter spawnings tend to have lighter egg deposition. Further, within a season, the mean spawning length changes: earliest spawnings are shorter than spawnings in the middle of the season; latest spawnings also tend to be shorter. Together these observations suggest that the earliest spawnings and latest spawnings are shorter and lighter than the majority of spawnings during the middle of the season.

Regulation of Intensity — A Hypothetical Mechanism

Perhaps the most striking aspect of herring spawn is the uniform egg density. Egg density appears to be generally consistent among herring stocks both in the Atlantic and Pacific (Table 4). Development and survival of inner egg masses in very thick spawn depositions are poorer relative to those closer to the surface. This is documented for North American Pacific herring (Taylor 1971; Hourston and Rosenthal 1981) and Asian herring (Galkina 1961).

The relationship between egg deposition and survival is not simply one of increasing egg mortality with increasing egg layers. For instance, Baxter (1971) found that overall egg mortality in Clyde herring spawns was low (less than 10%) and there was no obvious relationship between survival and the position of an egg in a layer, although the thickest spawns he examined had only eight layers. However, it is clear that exceptionally heavy egg depositions are deleterious to maximal egg survival. Among the thickest documented observations are 100 layers for Okhotsk Sea herring and 10 cm for California herring (Table 4). Such densities are unusual. However, because spawning aggregations can consist of many millions of fish, I suggest that it is surprising that even thicker densities are not found, for example, 500 or 1000 layers. The few relatively thick depositions that have been described (Table 4) are irregular. There must, therefore, be some biological mechanism regulating the intensity of egg deposition.

The number of layers of eggs in British Columbia spawnings rarely exceeds eight or nine and is most often only about two or three (Hourston and Haist 1981). The puzzle is how herring adjust their deposition so that density is low and uniform. Visual feedback seems impossible, particularly in spawning at night. Spawning both in the day and night is known to occur in British Columbia; night spawnings are documented in California (Spratt 1981). However, Holliday (1958) found that light retarded spawning behavior in Scottish herring. A tactile mechanism involving the gentical papilla could, theoretically, operate to reduce the egg intensity. For instance, it is clear that herring distinguish between different types of substrate (Haegele et al. 1981; Spratt 1981), and it is conceivable that they could distinguish between a barren surface and one covered with eggs. How, then, could these fish distinguish between a surface covered with two layers and another covered with four or five? An alternate explanation suggested here is that milt or sperm density might be a controlling factor. Stacey and Hourston (1982) demonstrated that addition of milt to tanks of captive herring sometimes induced spawning. They suggested

TABLE 4. Herring egg deposition intensities measured or assessed for different Pacific and Atlantic stocks.

Region or stock	Intensity (no. of egg layers or eggs/m^2 or comments)	Source(s)
Firth of Clyde	4–8 layers in thickest parts, 1–2 layers at edges	Parrish et al. 1959
Clyde	3–7 layers	Baxter 1971
Norwegian spring spawners	Thickest layers to 2.5 cm	Runnstrom 1941
North Sea	Observation of an abnormally thick piece of 3 cm	Hempel and Schubert 1969
Manx Island autumn spawners	300 000 to 1.6 million/m^2	Bowers 1969
Georges Bank (east coast of North America	1–2 cm over entire gravel substrate	Iles and Caddy 1972
White Sea spring spawners	Hundreds of thousands to millions/m^2 (3–10 layers)	Galkina 1971
Okhotsk Sea, Gizhiga Bay	Generally 3–5 layers with some locations reaching 15–20, or densities corresponding to 1–5 million/m^2	Galkina 1961
Okhotsk Sea	Exceptional densities up to 100 layers thick	Tyurnin 1973
California, San Francisco Bay	Maximally to 10 cm corresponding to 6 million/m^2	Spratt 1976
Southern British Columbia	Usually between 200 000 and 1 million eggs/m^2, rarely exceeding 4 million	From data presented in Haegele et al. 1979

that milt contains a sexual pheromone that promotes spawning by both sexes. It is plausible that as milt intensity increased, the positive feedback could be reversed to become a negative feedback to inhibit spawning. In low milt concentration, herring would continue to release milt and eggs; in high milt deposition concentration, fish would suspend spawning and move to adjacent locations with lower milt concentration. This suggestion is consistent with observations of sperm density by Hourston and Rosenthal (1976) that the sperm concentration was uniform over a wide geographic area of a spawning. Perhaps such uniformity represents an upper threshold that is sufficiently concentrated to inhibit further release of milt or eggs. A consequence of such a feedback mechanism is that egg layers would be greatest in locations where tidal current flushing is just enough to keep milt density low. Conversely, in areas of slow flushing and prolonged milt intensity, the egg intensity would be lower. These speculations are supported by observations of spawning herring in tanks at the Pacific Biological Station. These tanks are continuously flushed so that milt concentration is less than that of most natural spawnings; water in the tanks was never as discolored as it usually is in nature. Egg deposition is often in extremely dense bands, sometimes 20 or more layers, around the vertical sides of the tank and center standpipe. Therefore, in these conditions, a feedback mechanism could not work because the tank flushing keeps the milt concentration low.

Spawning Waves

Frequently there are two or more spawnings in some location separated roughly by 10–15 d. The later waves of spawning are similar to the first except that the later spawning fish are smaller and presumably younger. Size differences between waves were investigated in Barkley Sound, on the west coast of Vancouver Island, in 1982. Fish taken during the first wave (Fig. 9) were

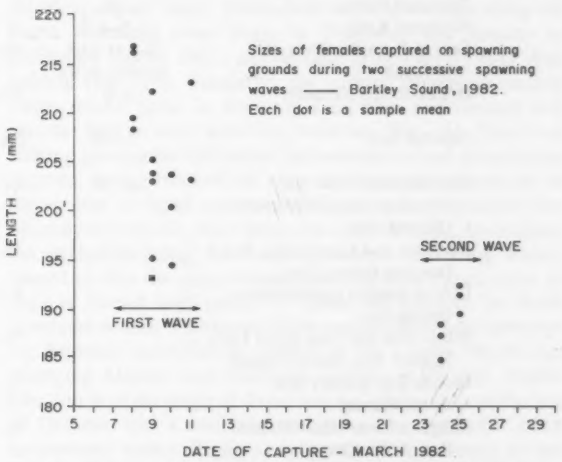


FIG. 9. Comparison of female lengths between the first and second wave of spawning in Barkley Sound (west coast of Vancouver Island) during March 1982. The first wave (March 7–12) consisted mainly of larger females; the second wave (March 24–25) consisted mainly of smaller fish between 170 and 190 mm standard length. Each point represents a sample mean. A total of 2797 females were sampled in roughly equal sample sizes.

TABLE 5. Comparison of spawning times, temperatures, and latitudes among Pacific herring stocks in North America, Asia, and the Arctic. Information for some locations was taken from several different sources, which sometimes conflicted, although never seriously. Estimates of temperature ranges for British Columbia were estimated by comparing unpublished records of spawning dates with records of sea surface temperatures.

	Eastern Pacific herring: south to north			
Region	Spawning temperatures (°C)	Latitude range (degrees)	Spawning period	Sources(s)
California	8–10	32–42	Oct.–Apr.	Alderdice and Velsen 1971; Scattergood et al. 1959; Miller and Schmidtke 1956
Oregon	4–12	42–46	Jan.–Apr.	Scattergood et al. 1959
Washington		46–49	Feb.–May	Chapman et al. 1941; Trumble 1979
Southern British Columbia	6–11	48–51	Jan.–May	Hourston 1980
Northern British Columbia	6–11	51–55	Mid-Jan.–June	Hourston 1980
Southeast Alaska	6–11	54–59	Apr.–May	Scattergood et al. 1959
South Central Alaska	—		Apr.–June	Moberly 1974; Alderdice and Velsen 1971
Prince William Sound, Alaska	—	60–61	Apr.—May	Rounsefell 1930
Cook Inlet, Alaska		59–61	Late Apr.–mid-May	Rounsefell 1930
Kodiak-Afognak Is., Alaska		57–58	Late May–early June	Rounsefell 1930
Alaska Peninsula, Bering Sea		55–56	Apr.–late May	Wespestad and Barton 1979; Barton and Wespestad 1980; Rounsefell 1930
Bristol Bay, Bering Sea		56–59	Mid-May–early June	Rounsefell 1930
Eastern Bering Sea (vicinity Nunivak Is.), Bering Sea		60–62	Late May–June	Rounsefell 1930
Norton Sound, Bering Sea		63–65	June	Rounsefell 1930
Port Clarence, Northern Bering Sea		65–66	June–early July	Rounsefell 1930
Kotzebue Sound, Arctic Ocean		66–67	July–mid-Aug.	Rounsefell 1930
Beaufort Sea (Tuktoyaktuk Harbor, Liverpool Bay)	0–5	69–70	June	V. Gillman, pers. comm.; Hunter 1975
Coppermine,[a] Coronation Gulf, Arctic Ocean	—	68–69		Hunter 1975
Southeast Korea	10		Late Dec.–Feb.	Kasahara 1961
Northeast Korea	0.5–4.5		Mar.–Apr.	Kasahara 1961
Gulf of Peter the Great–Sea of Japan	0–3 at start (mainly 4–9)	42–44	Mid-Mar.–early Apr.	Ayushin 1963; Dushkina 1973; Svetovidov 1952
Hokkaido and Sakhalin	3–6	43–50	Apr.	Dushkina 1973; Ayuishin 1963; Svetovidov 1952
Okhotsk Sea	2–10	56–60	Late May–mid-June	Dushkina 1973; Ayushin 1963; Svetovidov 1952
Gizhiginskaya Inlet and Shelekhov Bay (Northwest Okhotsk Sea)	2–10	59–62	Late May–early June	Dushkina 1973; Ayushin 1963; Svetovidov 1952
Korf Bay and Karaginskiy Bay (western Bering Sea)	2–7	58–61	Mid- to late May	Svetovidov 1952
Gulf of Anadyr (northwestern Bering Sea)		63–66	July	Svetovidov 1952
Tiksi Cove and Lena River Delta (Laptev Sea, Arctic Ocean)		72–74	?	Andriashev 1954 (cited in Riske 1960)
Olenek Bay (Laptev Sea, Arctic Ocean)		72–73	?	Svetovidov 1952
Indigirka River (East Siberian Sea, Arctic Ocean)		71–73		Svetovidov 1952
Ob Inlet[b] (Kara Sea, Arctic Ocean)		70–75	May until Sept.	Svetovidov 1952

[a]This is farther east than Cape Bathurst, indicated by Scattergood et al. (1959) as the "northern" limit of Pacific herring in North America.

[b]Svetovidov (1952) recognized these herring as a distinct group (*Clupea harengus pallasi* n. suworowi).

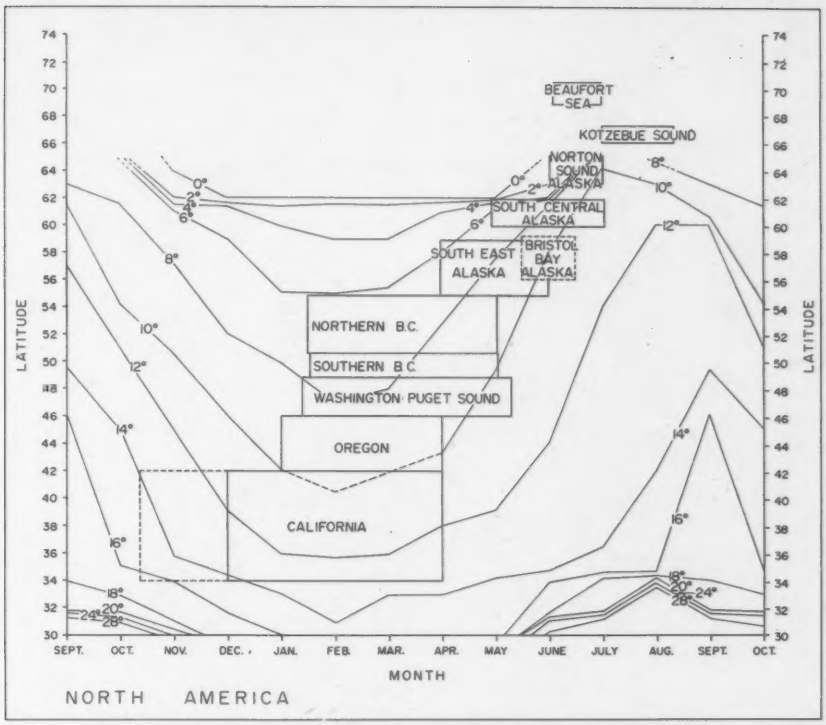


FIG. 10. Latitude, surface isotherms, and approximate spawning times and surface temperatures for North American herring. Most of the spawning occurs approximately between 6 and 10°C. Duration of spawning season appears to decrease in the north. Isotherms were calculated from Robinson (1976).

larger than those from the subsequent wave. There was also a third wave, approximately 2 wk later, but samples were not available.

The trend for large herring to spawn earlier seems to be widespread among stocks. It is described in California (Spratt 1981; Miller and Schmidtke 1956) and the Sea of Okhotsk (Svetovidov 1952) and some Atlantic herring (Blaxter and Holliday 1963). The genetic basis of different waves to each other is uncertain. Because smaller, younger fish are found in the later waves, it is likely that new recruits to the spawning stock participate mainly in later spawning waves. If so, then the two waves are part of the same stock. However, the spawning time of a stock is an adaptive characteristic, perhaps selected to provide the best match of emerging larvae to available food organisms in spring plankton blooms (Cushing 1975). It is not clear how natural selection could promote late spawning in recruits and early spawning among older, repeat spawners.

During the second wave spawning there are substantial numbers of spent fish, from the first wave, on the spawning grounds. Many of these spent fish have stomachs filled with eggs from second-wave spawners. Probably the herring filter-feed (see Blaxter 1985) to consume eggs that become detached from the substrate. Eggs can break loose and become suspended in the water column, particularly in spawning sites subjected to wave action, or after storms.

Spawn Timing: Temperature and Latitude

In general, spawn timing varies with latitude (Table 5). The earliest spawnings probably occur in the early fall in California, because larval herring have been found there in October (Eldrige and Kaill 1973). The latest may be in August in Bristol Bay (Table 5), or in July for the Queen Charlotte Islands (D. Hay, unpub. data). The earliest major spawnings along the North American coast begin in December and January in California (Spratt 1981) and become progressively later with latitude (Fig. 10). Similarly, the earliest spawnings among Asian stocks occur in Korea in December and January and become later in more northerly locations (Fig. 11). There is a striking geographic difference between the annual temperature regimes: during most of the year, isotherms are compacted in the vicinity of Japan and large differences in temperature can occur over relatively short distances (i.e. 1000 km). In contrast, the isotherms along the North American coasts are widely spaced so that the same temperature variation experienced in Asia is spread over nearly 10 times the distance in North American waters. This temperature pattern reflects the converging Kurishio and Oyashio currents in the western Pacific and diverging Alaskan and California currents in the east. Therefore, much of the range of Asian herring, particularly in the Sea of Okhotsk and Kamchatka waters, is in very cold, often ice-covered waters during early spring. These waters do not warm until May or June when most spawning occurs. Warming of these and Arctic waters occurs rapidly, in contrast with the earlier but slower temperature increase in British Columbia coastal waters. Therefore, with shorter growing seasons, which begin rapidly, northern and Arctic herring have probably adapted to spawning in colder waters. In the middle latitudes, particularly in North America, most spawning occurs between 6

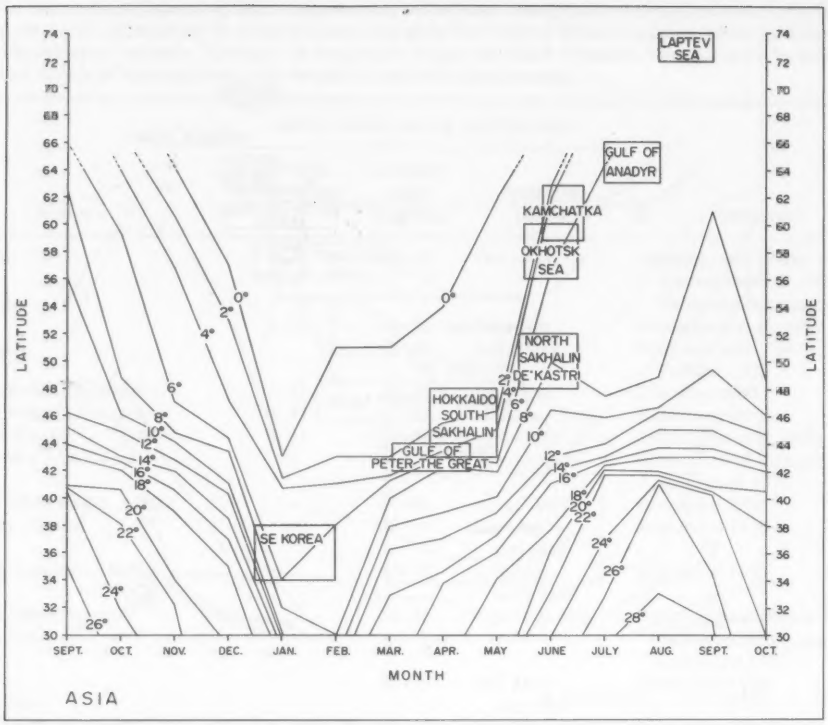


FIG. 11. Latitude, surface isotherms, and approximate spawning times and surface temperatures for Asian herring. Compared with North American herring at the same latitudes, most Asian herring spawn later probably because colder water penetrates farther south during the winter. Most Asian herring spawning occurs approximately between the 6 and 8°C. isotherms. Isotherms were calculated from Robinson (1976).

and 8°C isotherms. In California, most herring do not experience these temperatures and therefore must spawn in warmer waters.

Comparisons of spawn timing and egg size among Atlantic herring stocks (Bagenal 1971; Blaxter and Hunter 1982) reveal that the earliest spawners have the largest eggs. California herring, although being the earliest spawners, appear to have smaller eggs than more northern stocks. Perhaps the explanation for this apparent contradiction is that the common biological denominator among Pacific stocks varying in latitude is that they all spawn in their local spring and the timing of spawning is adjusted by selection to maximize larval survival during subsequent secondary production cycles. The local spring begins later in the north than in the south and some of the northern spawnings occur in cold water. Therefore, in a sense, some of these cold-water northern fish are ecologically early and chronologically late. In contrast, the California fish spawn chronologically early, but in temperatures typical of ecologically late spawnings in more northerly latitudes. Therefore, generalities relating spawning time and temperature must be within specific latitudinal ranges. This was done for the Strait of Georgia by relating monthly mean temperatures for March (Hollister and Sandnes 1972) to the annual mean date of spawning (in Julian days) calculated from Fishery Officer data. The result (Fig. 12) is a highly significant regression between the mean time of spawning and the mean annual temperature: the higher the temperature, the earlier the time of spawning.

An interesting exception to this general trend in spawn timing occurs in Naden Harbor, northern Queen Charlotte Islands. Here, a very early spawning, sometimes occurring in late January or early February, is observed most years. In contrast, other spawnings in the region occur mainly in April. One of the latest known spawnings also occurs in the Queen Charlottes: in Masset Inlet adjacent to Naden Harbor, where spawnings have been documented in late June and July. These two spawnings, which are geographically close, are among the extreme earliest and latest of British Columbia spawnings, respectively. Several other consistently late spawnings in May and June are typical of several inlets, such as Burke Channel, in the central area of the British Columbia coast.

These exceptional cases illustrate that spawning, even within local areas, is not wholly temperature dependent and other factors must also operate. For instance, Spratt (1981) claimed that most spawnings begin at periods of highest tides during darkness. Barton and Wespestad (1981) indicated that along the western Alaska coast the time of spawnings is associated with weather conditions and the associated ice breakup. These observations indicate that spawning might not follow immediately after fish reach physiological maturity; rather, spawning must require both physiological readiness and appropriate

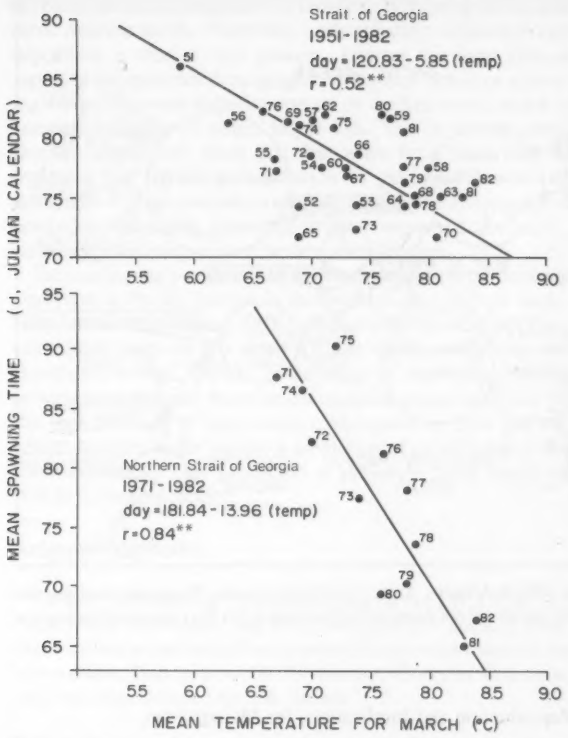


FIG. 12. Spawning time and temperature in the Strait of Georgia, B.C. The annual mean spawning time is inversely related to the monthly mean temperature for the month of March. Data on spawning time were from annual spawning reports, monthly mean temperatures were from Hollister and Sandnes (1972), and recent temperature data were provided by A. Dodimead of the Pacific Biological Station.

ecological cues. Such ecological cues are removed in experimental impoundments where herring can be held in a mature state for up to 40 d (Kreiberg et al. 1982; Brett and Solmie 1982). They can be held even longer in indoor tanks supplied with refrigerated seawater (D. Hay, unpubl. data).

Discussion

Reproduction, Recruitment, and Homing

Among the things we understand least about Pacific herring is the time and place during which recruits join the spawning population. Recruitment probably occurs mostly during age 3, particularly in southern British Columbia populations. Some 2-yr-olds also become sexually mature and join the spawning population. In northern British Columbia populations, some fish may not recruit until they are age 4 or 5. Nevertheless, the time and place where the recruits join the repeat spawners is not known although the problem would be clearer if we better understood the precise degree to which herring home. Blaxter and Holliday (1963) suggested that homing, to the extent that it occurs, is probably an effect of larval memory of the spawning grounds, a feat, they suggest, that would greatly exceed that of salmonids. After spawning, the adults depart to offshore feeding grounds and the eggs are left to incubate and hatch on the inter- and sub-tidal zones of the spawning beach. After several weeks, the eggs hatch and larvae tend to concentrate in the upper layers of the water column in the vicinity of the beach. Very little is known of the dispersal or survival of the larvae at this stage in their lives, but certainly they are widely separated from the migratory adult stock. After several months, and substantial mortality, the larvae metamorphose into juveniles. Little is known about the ecology or distribution of the 0-age group juveniles. They are found mainly inshore (Hourston 1959). Some are captured in exposed waters overlying the continental shelf but the proportion they represent of the cohort or their likelihood of survival are unknown. Further, it is not known whether juveniles from the Strait of Georgia or other areas migrate offshore or stay within the Strait for their first year. It is conceivable that some new recruits may not even migrate offshore but rather stay within the inshore waters until their first time of reproduction at which time they would meet the adult spawning generation for the first time. If they do migrate offshore as 1- or 2-yr-olds, it seems unlikely that they could avoid intermingling with juveniles from other stocks, in view of the limited areas of the continental shelf. However, on the basis of juvenile tagging experiments, Hourston (1959) concluded that juveniles do home, but to a lesser degree than adults (Hourston 1980). Nevertheless, it is not clear how the young recruits would be able to differentiate among the different spawning stocks that are on the banks: there are probably two or more migratory stocks from the Strait of Georgia and Puget Sound that would be offshore, and several stocks from the west coast of Vancouver Island. These stocks concentrate in similar offshore regions. It is not known whether different stocks are completely integrated in the offshore habitats. Catch analysis of offshore surveys indicates only that the different age or size groups tend not to be physically associated. If recruits do not physically join the main spawning stock in the offshore feeding locations, then it is possible that they make separate inshore migrations and rejoin the parent spawning stock on inshore wintering areas or when both groups return to the spawning locations.

Another consequence of the separation of prerecruits and their parental generation could be different rates of sexual maturity. If the development were too asynchronous it is conceivable that the two groups (recruit and repeat spawners) would not be able to spawn in the same time or even in the same place. If this were the case it could account for several different waves of spawning by different size groups (i.e. Fig. 9) that are frequently observed in various areas along the coast.

Reproduction and the Origin of Pacific Herring

Svetovidov (1952) distinguished Atlantic and Pacific herring as subspecies: *C. h. harengus* and *C. h. pallasi*, respectively. Based on ecological and morphological characteristics, each subspecies was then divided into "nationes" or forms. For instance, the White Sea herring were called *C. h. pallasi* n. *maris-abli* and Baltic herring were called *C. h. harengus* n. *membras*. This quardrinomial nomenclature is not recognized by the International code of Zoological Nomenclature (Berry 1964) and is not generally used even by subsequent Russian investigators (i.e. Nikolskii 1952). However, the general classification of Atlantic and Pacific herring into two subspecies tends to prevail among investigators, especially those working on Pacific herring. Svetovidov (1952) suggested that the Pacific form was derived from the spring-spawning herring of Arctic waters, which, in turn, were derived from spring spawning in

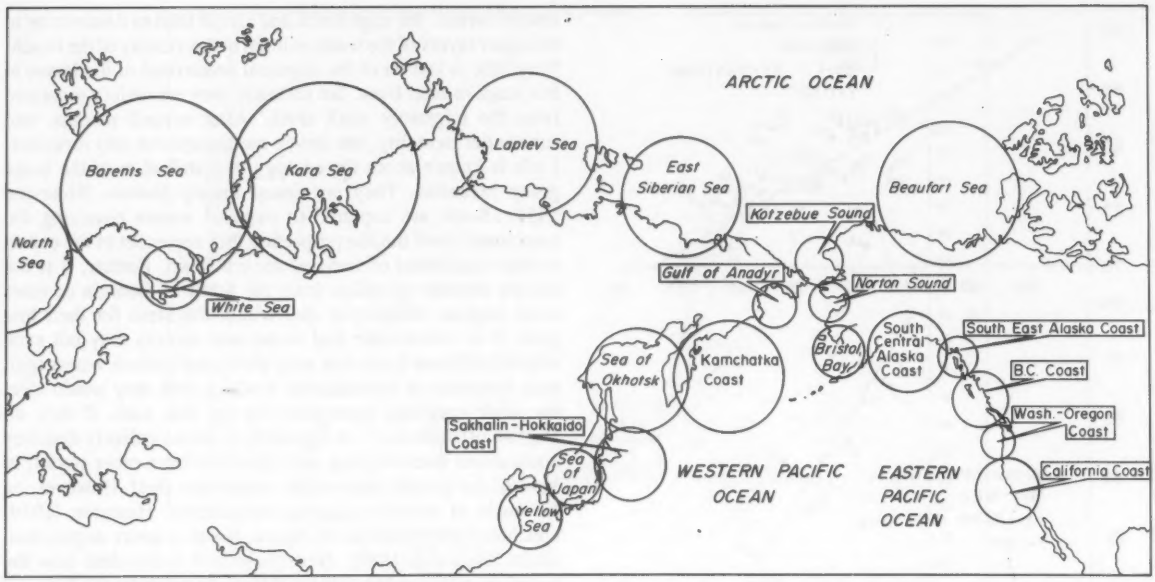


FIG. 13. Schematic view of the distribution of herring throughout the eastern North Atlantic, Arctic, and Pacific oceans. Spawning locations and distributions of Arctic herring are not well documented; therefore, sizes of the circles are not intended to represent either the range or abundance in these waters.

Atlantic herring. Subsequent to glacial recession, according to Svetovidov, the Arctic form recolonized temperate Pacific waters, but their inshore, spring-spawning habits represent genetic limitations imposed on the Pacific form from their Arctic ancestry.

An important aspect of Svetovidov's explanation is the apparent absence of fall-spawning herring, either on the North American or Asian coasts. Fall spawners in the Atlantic are generally found more in southern parts of the range, so genetic exchange between Atlantic fall spawners and Pacific herring does seem very unlikely. However, the claim that Pacific herring do not spawn in the fall because of a limited genetic capacity is weak. Spawn timing is an adaptive characteristic, selected to enhance egg and larval survival. Even within the same general locations, such as the northern Queen Charlotte Islands or San Francisco Bay, the earliest and latest spawnings can be nearly 6 mo apart, and over their entire range, Pacific herring spawn for nearly 10 mo. Presently, herring are almost circumpolar, with small disjunct populations in the North American and Eurasian Arctic coasts (Fig. 13). Arctic herring distribution seems to be associated with large rivers such as the Ob, Lena, and McKenzie. Such a distribution could represent relic populations from a once more widespread Arctic herring, and genetic exchange may well have been possible, as Svetovidov claimed. However, electrophoretic comparisons show distinct differences between Pacific and Atlantic herring (Grant 1981). There are also major differences among herring *within* their Pacific range: consider the October–November spawning in California, the July–August spawning in the Arctic, and even some semi-anadronomous spawners in Japan (Okada 1960). Other major differences among Pacific stocks occur in fecundity, growth rates, and longevity. These variations within Pacific herring appear to be as great as those between the Atlantic and Pacific.

Reproduction and Implications for Management

Presently in British Columbia and other areas in Pacific North America, herring are fished mainly for fish roe. This requires that herring be captured at the prime of their sexual maturity: close to or on the spawning grounds. To conduct these fisheries, it is desirable to be able to predict the time and location of spawning. Because spawning time is roughly related to temperature, we can now provide a general prediction that spawning times during warmer years will be earlier than in colder years. D. Ware (pers. comm.) is developing methodology that attempts to predict the precise time of spawning, within days, based on progressive changes in the GSI during the preceding month. Predicting the precise locations of spawnings is not yet possible, although there may be some trends associated with widespread climatic changes. For instance, it seems that spawning locations in warm years might differ from those of colder years (D. Hay, unpubl. data), but these analyses are still in progress.

A small but lucrative British Columbia fishery involves the production of "roe on kelp" (or more correctly, "spawn on kelp"). Herring are captured prior to spawning and transported live to temporary impoundments constructed of seine web and floats. Kelp fronds, usually *Macrocystis* sp., are suspended from the surface. When the operation is successful, herring spawn on the kelp fronds, which are then removed, brined, and prepared for human consumption. One of the most difficult problems associated with these operations is the initiation of spawning. Sometimes the impounded fish will not spawn, or spawn very lightly and yield a substandard product. This small industry could be greatly assisted if we could determine the exact environmental and biological conditions that trigger spawning.

Assessment of the magnitude of spawn deposition provides

the basis for stock assessment of most Pacific herring stocks and some Atlantic stocks. Therefore, understanding variation in egg deposition is vital to this process. Perhaps the most critical aspect is the apparent demographic difference between spawning waves. Most roe fisheries operate on the first wave, which is composed mainly of older, larger fish. Yet, in recent years, samples exclusively from this first wave have been used to represent the spawning population in general. This would introduce a bias towards underestimating the frequency of newly recruited fish spawning in later waves. Accordingly, sampling schedules require further consideration.

Estimating and predicting recruitment strength is particularly important in Pacific herring in the southern part of their range. Here, annual recruitment of 3- and 4-yr-old fish accounts for a substantial part of the stock (Tester 1955). Knowing the abundance of the recruits in advance of the fishery would provide a much firmer basis for decisions on annual harvests. To this end, analysis of age structure and maturity from fall and winter samples might permit a prediction of recruitment to the spawning stock. This procedure is presently being tested on British Columbia stocks.

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Life History Characteristics, Reproductive Value, and Resilience of Pacific Herring (*Clupea harengus pallasi*)[1]

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The energy supply available for growth and reproduction (surplus energy), fecundity, and egg size increase with female size in British Columbia stocks of Pacific herring (*Clupea harengus pallasi*). Fecundity is directly proportional to body weight, whereas egg weight is a curvilinear function with a weight exponent of about 0.2. The reproductive rate, defined as the product of fecundity and egg weight, is, therefore, proportional to the 1.2 power of the body weight. In 1974, 1978, and 1980 the size-dependent fecundity and reproductive rates were remarkably constant among management divisions along the coast. There is no evidence at present that these rates respond significantly to natural variations in stock abundance or marine climate. In contrast, there were interannual and regional differences in surplus energy that appeared as differences in the growth rate. Cluster analysis of the average length at ages 3–7 indicated that herring returning to the same division to spawn were more alike than those between divisions. An approximate reproductive value was calculated for the Queen Charlotte Island stock from the foregoing information, assuming that the population was momentarily at equilibrium. For the suspected natural mortality rate (M = 0.45), the maximum reproductive value occurred quite late in the life span: between ages 9 and 10. In other stocks of Pacific and Atlantic herring (*Clupea harengus harengus*), with adequate time series, the growth rates and hence weight-at-age have increased by as much as 50% in response to a combination of fishing and adverse environmental changes which reduced population size. Concurrently the age at first maturity fell by as much as 2 yr. It is argued that the maximum growth response of a herring population roughly defines its ability to stabilize itself. If the maximum compensatory response is a 50% increase in weight at age, the population should be able to sustain an annual exploitation rate between 0.2 and 0.3. In principle, at this level of harvesting the population will be as resilient to a short run of unfavorable conditions as an unexploited stock

Dans les stocks de hareng du Pacifique (*Clupea harengus pallasi*) de la Colombie-Britannique, l'énergie disponible pour la croissance et la reproduction (énergie supplémentaire), la fécondité et la taille des œufs augmentent en fonction de la taille de la femelle. La fécondité est directement proportionnelle au poids corporel tandis que le poids des œufs est une fonction curviligne dont l'exposant du poids s'élève à environ 0,2. Le taux de reproduction, soit le produit de la fécondité et du poids des œufs, est donc proportionnel au poids corporel à la puissance 1,2. En 1974, 1978 et 1980, les taux de fécondité et de reproduction dépendants de la taille étaient remarquablement constants entre les divisions gestionnelles de la côte. Il n'existe actuellement aucune preuve que ces taux réagissent de façon significative aux variations naturelles de l'abondance des stocks ou du climat marin. Par contraste, il y avait des différences interannuelles et régionales pour ce qui est de l'énergie supplémentaire, différences qui apparaissent comme des variations du taux de croissance. Selon une analyse par grappes de la longueur moyenne de trois à sept ans, les harengs qui retournent à la même division pour frayer se ressemblent plus que ceux de divisions différentes. À partir de ces données et en posant comme hypothèse que la population était momentanément en équilibre, on a calculé une valeur approximative du taux de reproduction du stock de l'île Reine-Charlotte. Au taux supposé de mortalité naturelle (M = 0,45), le taux maximal de reproduction apparaissait vers la fin de la vie, soit entre 9 et 10 ans. Dans les autres stocks de hareng du Pacifique et de l'Atlantique (*Clupea harengus harengus*) à séries chronologiques adéquates, les taux de croissance et donc le poids à un âge donné ont augmenté de jusqu'à 50 % en réaction à la pêche et à des conditions environnementales défavorables qui réduisaient la taille de la population. L'âge à maturité s'en trouvait abaissé de jusqu'à 2 a. L'auteur soutient que l'aptitude d'une population de hareng à se stabiliser est, d'une façon générale, régie par la réponse de croissance maximale. Si la réponse compensatoire maximale est une augmentation de poids de 50 % à maturité, la population devrait se maintenir quand le taux d'exploitation annuelle se situe entre 0,2 et 0,3. À ce taux, la population devrait normalement résister aussi bien qu'un stock non exploité à une courte série de conditions défavorables.

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In the eastern Pacific Ocean, Pacific herring (*Clupea harengus pallasi*) range from northern Baja California to Cape Bathurst in the Beaufort Sea. In waters off British Columbia, between six and nine populations have been recognized, and although some mixing occurs, these populations seem fairly discrete (Hourston 1980). Since the early 1950s the abundance of the British Columbia stocks has fluctuated around an average level of some 400 000 t (Stocker et al. 1983). In the mid-1960s, herring suffered a major coastwide reversal in abundance due to an intensification of fishing pressure and a run of poor year-classes. The fishery was subsequently closed to allow the stocks to rebuild. Fortunately, the remedial measures introduced by the fisheries managers of the day were successful, as most of the stocks regained their former levels of abundance by 1976 (Hourston 1980).

The primary life history characteristics of Pacific herring can be summarized by a few simple statistics. They rarely live more than 15 yr, and few longer than 9 yr. The maximum body size is about 550 g or 33 cm standard length. Like other relatively short-lived forms they mature early in life, typically in their second, third or fourth year, and produce about 190 eggs/g annually. With only minor exceptions, the stocks on both sides of the Pacific spawn during the local spring. Despite differences in longevity between races of Atlantic (*Clupea harengus harengus*) and Pacific herring, Beverton (1963) observed that they all tend to reproduce for approximately 68% of their life span. In view of the clear association between reproductive drain and natural death in short-lived clupeids, Beverton (1963) speculated that maturation may be more closely related to longevity in this group than growth seems to be.

In a recent review, Murphy (1977) remarked that life history characteristics such as fecundity, age at first reproduction, and life span "are not biological curiosities but rather are closely related and are of great adaptive significance with respect to the success of a species in its ecosystem." For relatively short-lived fishes, some exploratory calculations (Ware 1984) suggest that a constant reproductive rate, determined strictly by body size at the time of spawning, tends to produce the highest fitness, in an evolutionary sense, when there is a survival cost (Calow 1979) associated with reproduction. This strategy, however, is not particularly adaptive for long-lived species. Where there is an effect the evidence indicates that fecundity tends to be weakly density dependent in Atlantic and Pacific herring (Ware 1980). The possibility that it might be slightly stronger in longer lived clupeid stocks apparently has not been examined.

The pattern of reproduction raises some other fundamental concerns about population dynamics. For instance, it has been suggested that because herring are not very fecund they should be more vulnerable to climatic change and fishing mortality than gadid species, which have a greater capacity for stabilizing their numbers under random fluctuations (Cushing and Harris 1973). Within this context this paper considers how British Columbia herring allocate energy to growth and reproduction, and highlights some of the management implications. Finally I touch on the effect of a fishery on growth and the age at first reproduction, and show that the limited capability of herring to alter these characteristics allows the stocks to compensate for an exploitation rate of only 0.2–0.3.

Data, Methods, and Definitions

The 1974 and 1978 fecundity data referred to in this report are described in detail by Hourston et al. (1981). In 1974, ovaries were collected from 3061 females, and from 1063 females in 1978 during regular sampling of the British Columbia commercial roe herring catch. The 1980 samples (1697 females) were analyzed by D. Hay (pers. comm.) using similar methods as Hourston et al. (1981). With the exception of 1978, the ovaries were weighed fresh and preserved in Gilson's fluid for a minimum of 6 wk. Average egg weight was estimated by dividing the fresh ovary weight by the fecundity, which was determined by a gravimetric method. Unfortunately, fresh ovary weights were not recorded in 1978, so only the fecundity data were available for analysis.

Hourston et al. (1981) found that female weight at spawning explained 70% of the variation in fecundity among individuals. They concluded that while fecundity estimates based on body weight, length, and age would be most reliable (accounting for 72% of the variation), estimates based on weight alone would be only marginally less so. Hence, total weight was chosen as the dependent variable for this anaylsis.

The British Columbia coast has been divided into six management divisions, which contain reasonably discrete spawning stocks (Fig. 1). These divisions in turn have been subdivided into 35 management units which support individual roe fisheries (Hourston and Hamer 1979). The pattern of energy allocation in each management unit was determined by blocking the sampling data by age like the example shown in Table 1. For these analyses I have assumed that herring spawn on their birthday. Thus, the 3-yr-old fish in Table 1 are exactly 3 yr old and are about to enter their fourth growing season. With this aging convention in mind, we can adopt the following definitions and symbols:

X = age (yr)
L_x = mean standard length (cm) at end of age X (i.e. at spawning)
W_x = mean total weight (g) at spawning
R_x = mean reproductive rate, which is equal to the ovary weight at spawning (g/yr)
WS_x = mean somatic weight (g) at beginning of age X. Hence, $WS_x = W_{x-1} - R_{x-1}$
$\bar{W}_x$ = midyear weight during age $X = (WS_x + W_x)/2$
ΔW_x = growth rate (g/yr)
S_x = surplus energy supply (g/yr) during age $X = \Delta W_x + R_x$
b_x = mean fecundity at spawning (yr^{-1})
θ_x = mean egg weight (g) at spawning = R_x/b_x

It is apparent from the foregoing definitions that surplus energy (s_x) represents the annual supply available for growth and reproduction at each age after all maintenance and activity costs have been discounted. In practice, estimates of S_x therefore depend, in part, on the accuracy of the estimated somatic growth rate:

$$(1) \quad \Delta W_x = (W_{x+1} - R_{x+1}) - (W_x - R_x).$$

This formula assumes that the mean somatic weight of all year-classes in the sample is the same at the beginning of each age. Since growth can vary with population density and a number of other environmental factors, this assumption is unlikely to be true. The resulting estimates of ΔW_x are therefore slightly biased but not in a systematic direction, for the growth rate is just as likely to be overestimated as underestimated.

Ideally, ΔW_x and S_x should be calculated for either a single year-class over its life span or from weight-at-age data averaged over a number of years to reflect the typical growth of

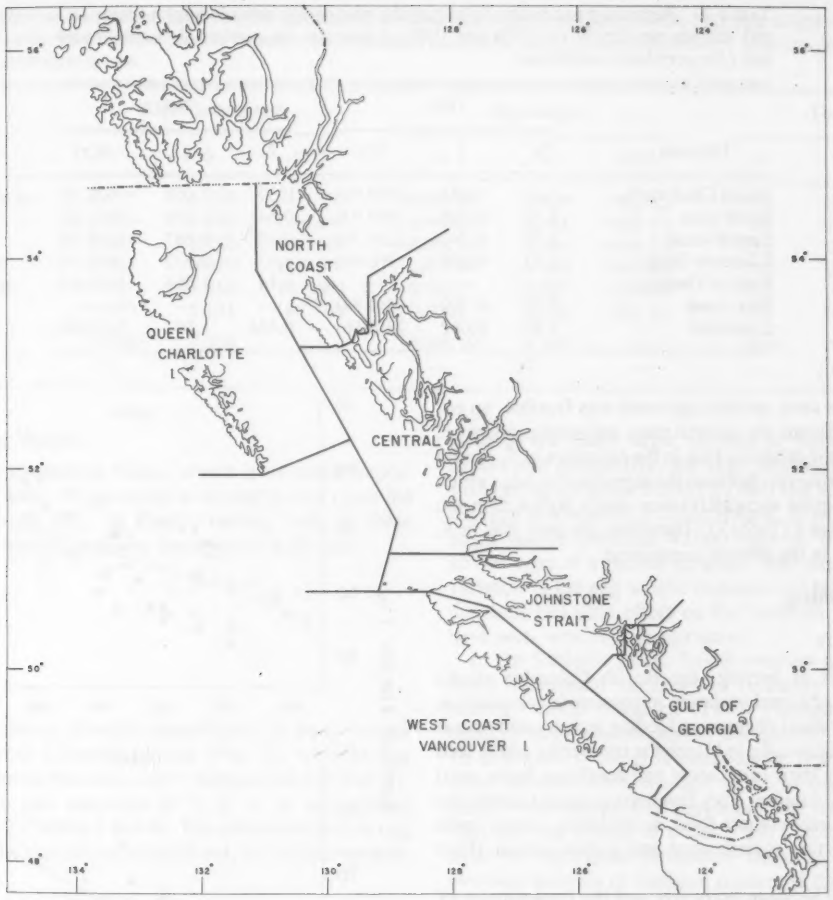

FIG. 1. British Columbia herring management divisions. Note that the Gulf of Georgia is also called the Strait of Georgia Division.

TABLE 1. Example showing how to block the sampling data to calculate the midyear weight, growth rate, and surplus energy supply. This sample came from Skincuttle Inlet (Queen Charlotte Island Division, Management Unit 5) in 1974. The tabulated values show the means for each age group.

Age (yr) X	Standard length (cm) L_{x-1}	Total weight (g) W_{x-1}	Somatic weight (g) WS_x	Reproductive rate (g/yr) R_{x-1}	Midyear weight (g) W_x	Growth rate (g/yr) ΔW_x	Surplus energy (g/yr) S_x
3.0	19.87	96.7	73.3	23.4			
					106.2	28.0	65.7
4.0	21.71	139.0	101.3	37.7			
					136.0	20.9	69.3
5.0	23.14	170.6	122.2	48.4			
					165.0	23.8	85.5
6.0	24.09	207.7	146.0	61.7			
					188.2	14.3	84.3
7.0	25.10	230.3	160.3	70.0			

TABLE 2. Regression parameters describing the relationship between surplus energy (S_x) and midyear weight ($\bar{W}_x$) in 1974 and 1980. N indicates the number of sample means and r the correlation coefficient.

Division	1974			1980		
	δ	ζ	$N(r)$	δ	ζ	$N(r)$
Queen Charlotte Is.	3.22	0.631	10(0.91)	0.39	1.068	9(0.79)
North coast	2.10	0.718	6(0.83)	0.34	1.076	10(0.92)
Central coast	1.58	0.742	22(0.70)	2.12	0.687	12(0.76)
Johnstone Strait	2.73	0.608	9(0.66)	3.02	0.575	6(0.75)
Strait of Georgia	—	—	—	0.14	1.266	10(0.84)
West coast	2.09	0.702	14(0.84)	—	—	—
Combined	2.40	0.662	73(0.66)	0.414	1.042	54(0.86)

population. In this case, neither approach was feasible, so eq. (1) was used to estimate the growth rates and surplus energy. I hasten to add that the resulting bias in the estimates of S_x should not be too great, however, because the reproductive rate (which can be estimated quite accurately) was much higher than the growth rate after age 4 (Table 1). Therefore, the only bias in S_x is due to the error in the growth component.

Energy Partitioning

Rate of Expenditure

Like most races of herring, the British Columbia stocks undergo a marked seasonal variation in proximate composition that is linked to cyclical changes in feeding activity and sexual maturation. After spawning in March the recovering adults feed heavily, increasing their oil content and condition factor until late summer–early autumn. Very few herring caught during the late autumn and winter contain food, so evidently, stored lipids are used in supporting maintenance and gametogenesis (Hart et al. 1940).

The relationship between body size and the total amount of energy available for growth and reproduction in 1974 and 1980 is shown in Fig. 2. Despite the random variation that has already been discussed, the supply of surplus energy clearly increased with female weight:

$$S_x = \delta W_x^{\zeta}. \quad (2)$$

The value of the weight exponent in eq. (2) was higher on average in 1980 (Table 2) because herring over 140 g from the Queen Charlotte Islands, North Coast, and Strait of Georgia divisions had larger supplies of surplus energy at the end of the 1979 growing season. For instance, a 190-g fish in the spring of 1980 had stored 98 g of surplus energy compared with 77 g in 1974. This represents a 27% increase and highlights the fact that S_x depends on factors other than body weight, such as local environmental conditions and possibly stock density.

Reproductive Rate

The reproductive rate (R_x), defined earlier as the ovary weight at the end of age X, has the dimensions of grams per year. Like surplus energy, it also increases as a power function of body weight:

$$R_x = cW_x^{\phi}.$$

Note that by using this expression we are simply describing how the size of the ovary at spawning increases in relation to the body weight. It is significant that for a given female size the reproductive rate was practically identical between management divisions and years (Fig. 3). This is also apparent if one compares the fitted parameter values listed in Tables 3 and 4. In fact, the small amount of scatter about the regression lines in Fig. 3 leaves little doubt that the ovary weight of British Columbia herring is a very conservative property. It is primarily a function of the size of the female at spawning and is not affected to a significant extent by interannual and regional variations in environmental conditions or stock abundance, at least over the observed range. This observation has important management implications that we will return to later, but first we must consider the fate of the resources allocated to reproduction.

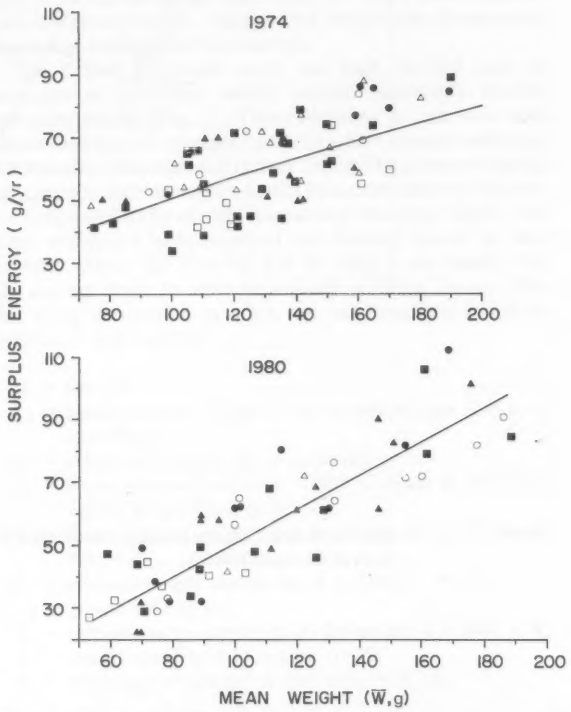

FIG. 2. Relation between surplus energy and the estimated midyear weight ($\bar{W}_x$) by division. ●, Queen Charlotte Islands; ○, north coast; ■, central coast; □, Johnstone Strait; ▲, Strait of Georgia; △, west coast Vancouver Island.

TABLE 3. Regression parameters describing the relationship between total weight, reproductive rate (R_x), egg weight (θ_x), and fecundity (b_x) in 1974. N indicates number of sample means, r the correlation coefficient, and C.V. the coefficient of variation. Values marked with an asterisk are geometric means.

Division	Reproductive rate			Egg weight			Fecundity		
	c	ϕ	$N(r)$	a	γ	$N(r)$	k	β	$N(r)$
Queen Charlotte Is.	0.055	1.323	14(0.99)	0.00016	0.434	14(0.82)	358	0.884	14(0.97)
North coast	0.079	1.243	10(0.99)	0.00083	0.111	10(0.41)	95	1.134	10(0.97)
Central coast	0.069	1.283	30(0.99)	0.00031	0.301	30(0.77)	219	0.982	30(0.99)
Johnstone Strait	0.343	0.959	14(0.96)	0.00090	0.092	14(0.42)	380	0.866	14(0.95)
Strait of Georgia	0.114	1.168	12(0.99)	0.0002	0.387	12(0.87)	555	0.782	12(0.97)
West coast	0.075	1.271	19(0.99)	0.0003	0.276	19(0.81	219	0.997	19(0.98)
Mean	0.098*	1.208	—	0.00036*	0.267	—	265*	0.941	—
C.V. (%)	—	11	—	—	53	—	—	13	—

Fecundity vs Egg Weight

Excluding the connective tissue, which is of minor importance, the ovary mass (R_x) is equal to fecundity (b_x) times the average egg weight (θ_x). In Pacific herring both of these variables can be treated as power functions of body size:

(3) $\theta_x = aW_x^{\gamma}$

(4) $b_x = kW_x^{\beta}$.

Hence

(5) $R_x = akW_x^{\beta+\gamma}$.

Fecundity is almost directly proportional to body weight amongst the British Columbia stocks (Fig. 4), whereas egg weight is a curvilinear function, with γ being about 0.2 (Fig. 5). The reproductive rate exponent ($\theta = \beta + \gamma$) is therefore approximately 1.2 (Tables 3 and 4). The observed trend in egg weight with female size, though significant, is clearly overshadowed by the much larger increase in fecundity. To put these factors into perspective, the eggs produced by an 80-g recruit spawner weigh about 0.0012 g (wet) and are 25% smaller than the eggs produced by a 220-g female. In terms of fecundity the larger female produces 42 000 eggs or 180% more than the 15 000 eggs of a recruit spawner. This explains why the high variation in the egg weight exponent (γ) between management divisions had little effect on the variation in ϕ, which, as we have seen, was very conservative.

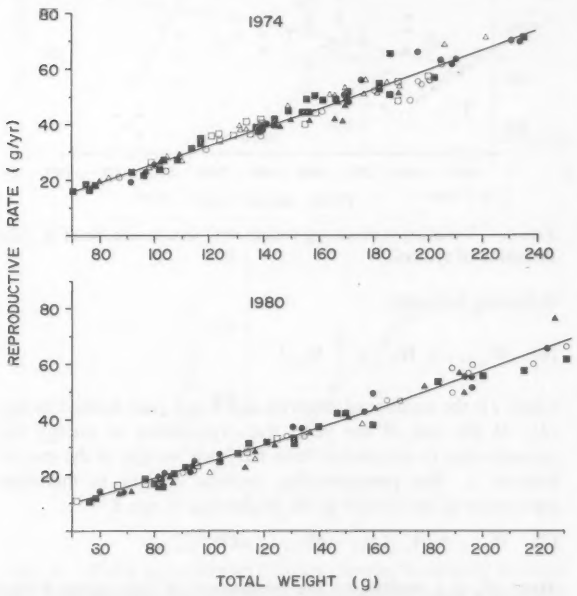

FIG. 3. Reproductive rate of British Columbia herring in 1974 and 1980. In this case the annual reproductive rate is equal to the ovary weight at spawning. See Fig. 2 for definition of symbols.

In the Sakhalin stock, Soviet workers have reported significant interannual variations in fecundity for a given size of herring, which Nikolskii (1969) claimed can be linked to changes in population density and general feeding conditions. To determine if the differences in the reproductive characteristics between divisions and years in the British Columbia stocks were statistically significant, the ovary weight, fecundity, and egg weight of a 160-g fish (Table 5) were estimated from the regression parameters listed in Tables 3 and 4. A two-way analysis of variance confirmed that the variation was random. Thus, in contrast with the Sakhalin stock, the fecundity and egg size of British Columbia herring were relatively insensitive to whatever differences there were in abundance (Stocker et al. 1983) and local climate in the various management divisions in the 1973, 1977, and 1979 growing seasons. Although a more detailed analysis of covariance indicates that there were subtle differences between divisions, and within divisions between years, these differences tended to be small and therefore not very significant from a biological standpoint. We should not rule out the possibility, however, that differences in fecundity might become more pronounced if the stocks experienced a sharp decline in abundance or unusual environmental conditions.

Though there is a hint in Table 5 of a possible trade-off between mean fecundity and egg size among management divisions, this negative correlation probably is not real. A detailed study of the maturation process in Barkley Sound herring revealed that egg weight increased up to the time of spawning, while the mean fecundity decreased (D. M. Ware, unpubl. data). Since females at the same age and state of maturity (i.e. same gonosomatic index) in Barkley Sound had similar egg weights, it follows by analogy that the negative correlation between fecundity and egg weight in Table 5 may reflect a general sampling problem. Presumably, fish from the various divisions were in slightly different maturity states at capture; if they had been in the same state the fecundities and egg weights might have been even more similar (see Hay 1985).

TABLE 4. Regression parameters describing the relationship between total weight, reproductive rate (R_x), egg weight (θ_x), and fecundity (b_x) in 1980. N indicates the number of sample means, r the correlation coefficient, and C.V. the coefficient of variation. Values marked with an asterisk are geometric means.

Division	Reproductive rate			Egg weight			Fecundity		
	c	ϕ	$N(r)$	a	γ	$N(r)$	k	β	$N(r)$
Queen Charlotte Is.	0.089	1.222	14(0.99)	0.00095	0.068	12(0.32)	93	1.156	12(0.99)
North coast	0.068	1.274	7(0.99)	0.00088	0.090	7(0.48)	86	1.162	7(0.99)
Central coast	0.106	1.179	16(0.99)	0.00045	0.232	16(0.85)	236	0.949	16(0.98)
Johnstone Strait	0.088	1.224	8(0.99)	0.00042	0.255	8(0.71)	212	0.968	8(0.97)
Strait of Georgia	0.033	1.416	16(0.99)	0.00029	0.298	15(0.89)	111	1.120	15(0.99)
Mean	0.071*	1.263	—	0.00054*	0.189	—	134*	1.071	—
C.V. (%)	—	7	—	—	55	—	—	10	—

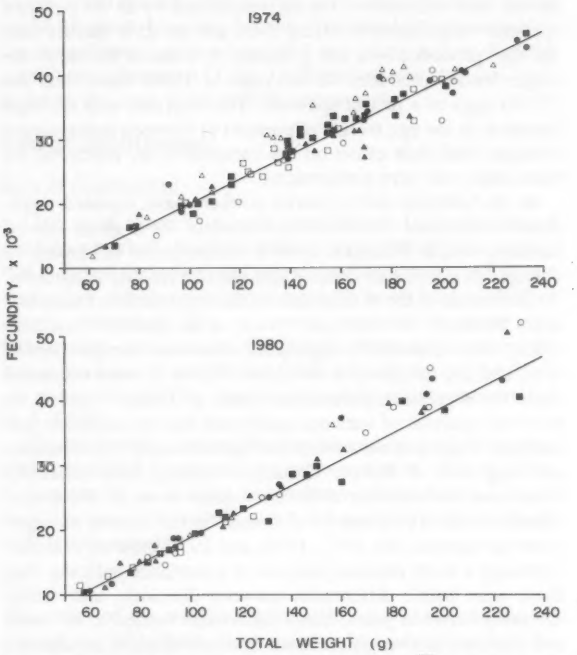

FIG. 4. Fecundity in relation to female weight at spawning. See Fig. 2 for definition of symbols.

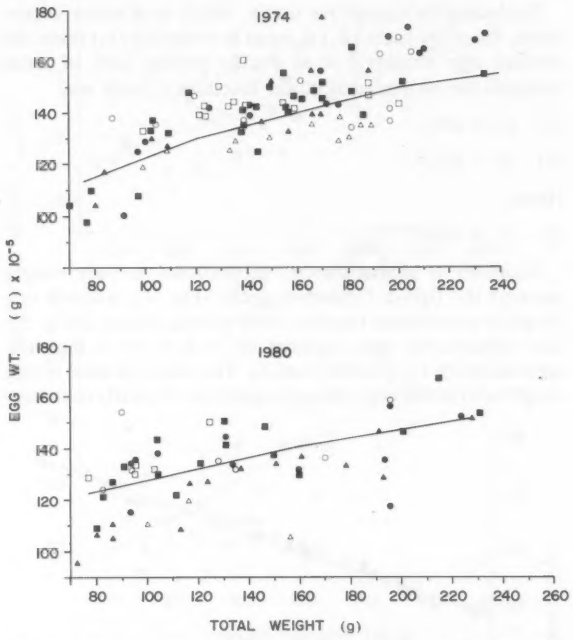

FIG. 5. Variation in mean egg weight with female size. See Fig. 2 for definition of symbols.

Growth Rates and Size at Age

The annual growth rate (grams per year) was defined above as the residual supply of surplus energy after spawning. Since it has been shown that the size-dependent reproductive rate is remarkably constant, it follows that the between year and age variation in surplus energy must appear as differences in growth. Herring produce only one batch of eggs per year and spawn over a relatively short period, so it is reasonable to treat their growth and reproduction dynamics as discrete time processes. The size at age can be calculated from the equations governing energy expenditure by dividing a year into a number of small, equally spaced intervals of, say, 1 wk. If $W(x, i)$ is the body weight at the beginning of interval i, the size at the beginning of the next interval can be approximated by the following formula:

$$(6)\quad W_{x,i+1} = W_{x,i} + \frac{\delta}{t} W_{x,i}^{\zeta}$$

where t is the number of intervals and δ and ζ are defined by eq. (2). At the end of the year, the expenditure of energy for reproduction is subtracted from the body weight at the end of interval t. The postspawning somatic weight is therefore equivalent to the weight at the beginning of age $X + 1$:

$$(7)\quad W_{x+1} = W_{x,(i=t)} - P_{x,(i=t)}\, akW_{x,(i=t)}^{\beta+\gamma}.$$

Here, $P_{x,(i=t)}$ represents the proportion of age group X that matures in interval t.

Given reliable parameter estimates, eq. (6) and (7) can be solved iteratively to obtain the body weight at spawning (Fig.

TABLE 5. Mean fecundity ($\bar{F}_{160}$), egg weight ($\bar{\theta}_{160}$), and ovary weight ($\bar{\theta}\bar{F}_{160}$) of a 160-g herring from various management divisions in 1974, 1978, and 1980. C.V. is the coefficient of variation.

Division	1974			1978	1980		
	$\bar{F}_{160}$	$\bar{\theta}_{160}$	$\bar{\theta}\bar{F}_{160}$	$\bar{F}_{160}$	$\bar{F}_{160}$	$\bar{\theta}_{160}$	$\bar{\theta}\bar{F}_{160}$
Queen Charlotte Is.	31 792	0.00145	46.1	29 598	32 843	0.00134	44.0
North coast	30 005	0.00146	43.8	26 945	31 310	0.00139	43.5
Central coast	31 980	0.00143	45.7	29 484	29 149	0.00146	42.6
Johnstone Strait	30 770	0.00144	44.3	33 413	28 794	0.00153	44.1
Strait of Georgia	29 358	0.00143	42.0	28 505	32 582	0.00132	43.1
West coast	34 478	0.00138	47.6	30 040	—	—	—
Mean	31 397	0.00143	44.9	29 664	30 936	0.00141	43.4
C.V. (%)	5.8	1.9	4.4	7.2	6.1	6.2	1.5

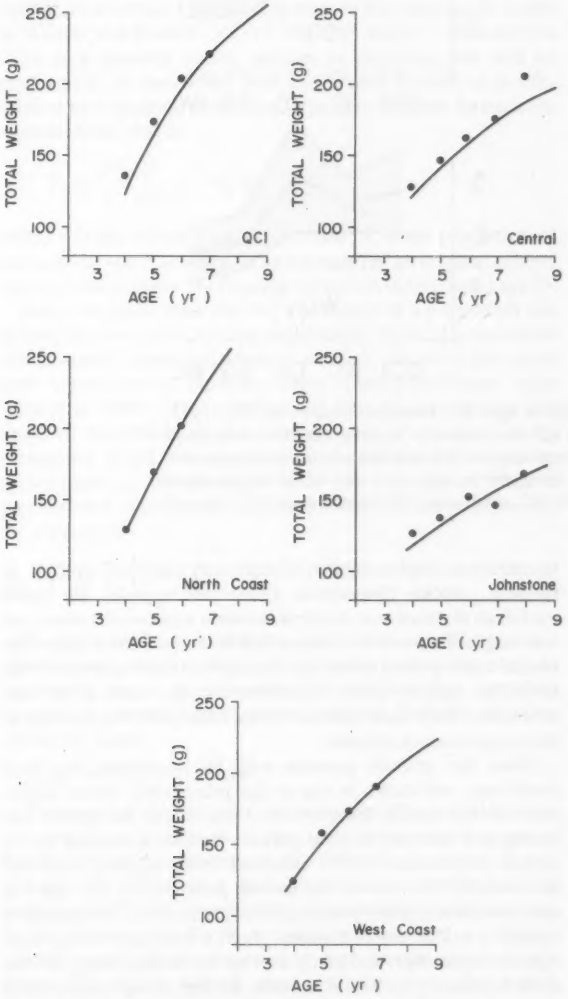

FIG. 6. Size at age of British Columbia herring in different divisions in 1974. The data points identify the observed body weight at the end of each age (before spawning). The curves show the corresponding weights predicted by eq. (6) and (7), using the parameter estimates in Tables 2 and 3 for each division. See text for details.

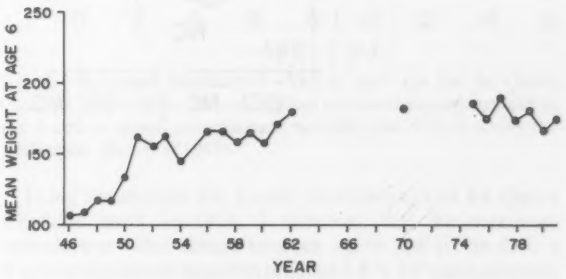

FIG. 7. Long-term change in the mean weight of 6-yr-old herring in the winter of their seventh year of life (age VII in the old aging system) in the north coast division. The 1946–62 data were compiled during the days of the reduction fishery (Pacific Biological Station, unpubl. data).

6). The resulting pattern indicates that the Queen Charlotte Islands and North Coast herring currently grow at higher rates after age 4 than the Johnstone Strait and central coast groups, whereas fish from the west coast of Vancouver Island grow at intermediate rates.

What Fig. 6 does not show is that the size at age has changed significantly in some stocks in the last 50 yr. In the 1930s, Tester (1933) reported that herring caught in the vicinity of Prince Rupert were smaller than those from southern British Columbia at all ages. Indeed the most striking increase in size has taken place in the North Coast division (specifically management sections 31, 41, and 51, which correspond to the old Northern Straits subpopulation). Between 1949 and 1962 the average weight of a 6-yr-old herring in the late fall of its seventh growing season in this area increased 72%, from 110 to 189 g (Fig. 7). This trend broadly parallels the development of the North Coast fishery, where the average catch rose abruptly from about 8000 t in 1947 to 26 000 t from 1948 to 1965 (Hourston 1980). Recent assessments indicate that this stock did not fully recover from the decline in the late 1960s and is currently at a low level of abundance. The size at age is still high compared with historical levels, suggesting that the growth rate continues to reflect the low abundance of the stock.

In the next section I will try to put the foregoing observations on herring growth and reproduction into a management context by touching specifically on the apparent distribution of the stocks, their reproductive value, and resilience.

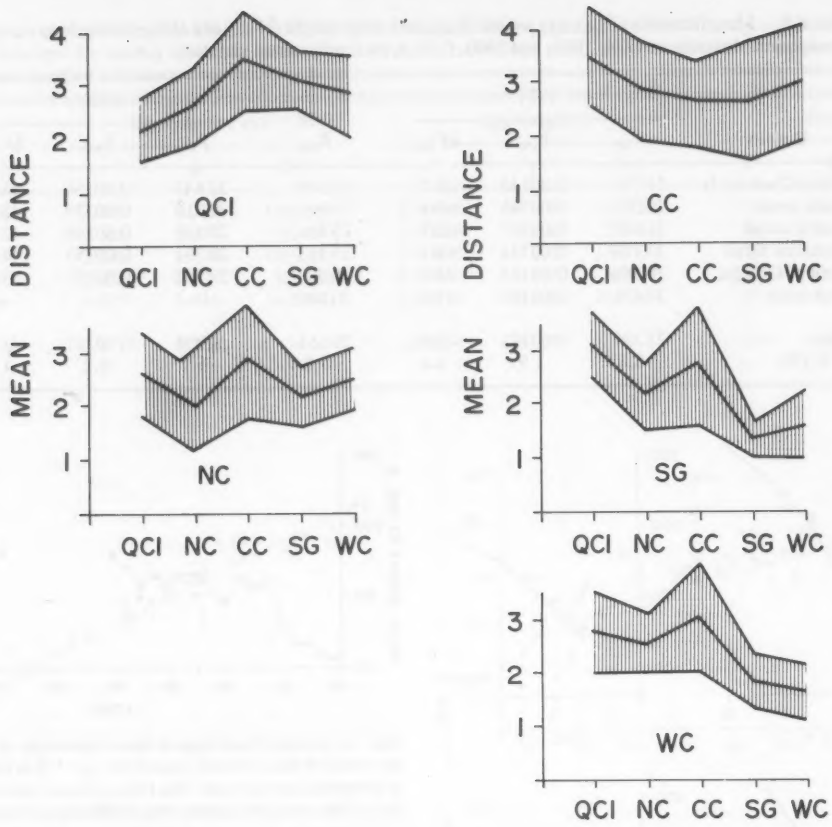

FIG. 8. Mean euclidean distance in observed lengths at ages 3–7 between divisions in 1972, 1975, 1978, and 1980. For this analysis the lengths at each age were treated as variables and the management units as cases. The midline shown above represents the average euclidean distance between management units in each division, whereas the top and bottom lines join the maximum and minimum calculated distances, respectively. QCI, Queen Charlotte Islands; NC, north coast; CC, central coast; SG, Strait of Georgia; WC, west coast of Vancouver Island.

Implications

Stock Separation

British Columbia herring have been classified into spawning stocks on the basis of vertebral counts and tagging studies. To complement these more direct methods, a cluster analysis of the average lengths at ages 3–7 (variables) within 19 management units (cases) was performed to determine whether the growth pattern could be used as a rough index for stock identification. Four years of length data were available for these 19 cases (Hourston 1981). For each year the mean euclidean distance, i.e. the square root of the sum of squares of the differences between the values of the variables for two cases, was calculated for all combinations. The results were subsequently pooled by management division.

The mean euclidean distance between the lengths at age within a division was consistently smaller than the distance between divisions (Fig. 8), indicating that the stocks are somewhat discrete and that herring that return to the same division to spawn are more alike than those between divisions. There remains, however, considerable heterogeneity within some divisions, particularly the central coast which is suspected to contain a complex mixture of migratory and nonmigratory, or resident, stocks (Stevenson 1946). As a rule, the mean euclidean distance was smallest between adjacent divisions and was largest between well-separated divisions. Once again, the central coast proved to be the exception as three quarters of the divisions, namely Queen Charlotte Islands, north coast, and west coast, were least like the central coast probably because of the complex stock mixture.

Since the growth process will be modulated by local conditions, variations in size at age presumably reflect differences in the spatial distribution of the stocks during the late spring and summer feeding period. Indeed, according to the picture Stevenson (1955) obtained from tagging, and the divisional differences in the growth pattern (Fig. 8), one can speculate that migratory herring from the Strait of Georgia move farthest south on the continental shelf, where they forage from April to September, and partly overlap the feeding range of west coast herring. This would account for the strong resemblance between these divisions. In contrast, the central coast division consists of a mixture of migratory and resident stocks that are believed to spend the summer feeding at varying distances from the coast. The generally poorer production of food near shore may explain why some of the resident stocks grow more slowly

than the migratory stocks (Stevenson 1946) and hence why the within-division growth patterns in this case are so heterogeneous. Herring from the north coast and Queen Charlotte Islands spawning stocks are thought to feed in Dixon Entrance, Hecate Strait, and off Cape St. James (Taylor 1970). The resemblance between the average lengths at age of Strait of Georgia and North Coast herring suggests that the latter may move farther south to feed than the Queen Charlotte Islands stock. Although the foregoing interpretation is speculative, it indicates that the growth pattern contains some circumstantial information on distributions and degree of mixing that can be used in association with other characteristics for stock identification.

Reproductive Value

The concept of reproductive value has played a pivotal role in linking life history studies and evolutionary biology. A particularly lucid account of the development of this idea can be found in Wilson and Bossert (1971). Put very simply, reproductive value is a measure of the number of offspring that will be produced by an individual from age X until the end of its life, relative to a newborn individual. The discrete time formula for reproductive value is

$$(8)\quad V_x = \frac{e^{rx}}{l_x} \sum_{y=x}^{\infty} e^{-ry} l_y m_y$$

where r is the intrinsic rate of increase, l_x is the proportion of survivors at age X (both male and female) of an original cohort, and m_x is the number of offspring born to an individual at age X.

It is a truism to state that the abundance of a population can neither increase nor decrease indefinitely. Natural populations are constantly being perturbed by extrinsic variables that cause their abundance to fluctuate about some equilibrium value (Lewontin 1969). Over a sufficiently long period, positive and negative excursions in the intrinsic rate of increase of the population about the equilibrium should cancel, so as an approximation, the average value of r is zero. When a population is momentarily at its stable equilibrium position, eq. (8) reduces to

$$(9)\quad V_x = \frac{1}{l_x} \sum_{y=x}^{\infty} l_y m_y.$$

To estimate the reproductive value from eq. (9) one must specify how survivorship and fecundity vary with age. In calculating m_x, it is customary, for animals that reproduce bisexually, to credit each parent with one half the offspring produced; hence

$$m_x = b_x/2 = (c/2a)W_x^{\phi-\gamma}.$$

The age-specific mortality rate is more problematical because not enough is known about the larval and juvenile stages of Pacific herring. To circumvent this difficulty the life cycle was divided into two parts: a premature phase where the instantaneous mortality rate from birth to sexual maturity was presumed to be constant (M_1) and an adult phase where a different mortality rate (M) was assumed to apply for the rest of the life span. The oldest herring ever recorded from the British Columbia fishery is 15 yr (Pacific Biological Station, unpubl. data), so this was taken to be the maximum age. Thus, for any arbitrary value of M and abundance at maturity, one can calculate the initial number of progeny and, hence, M_1 and finally the reproductive value.

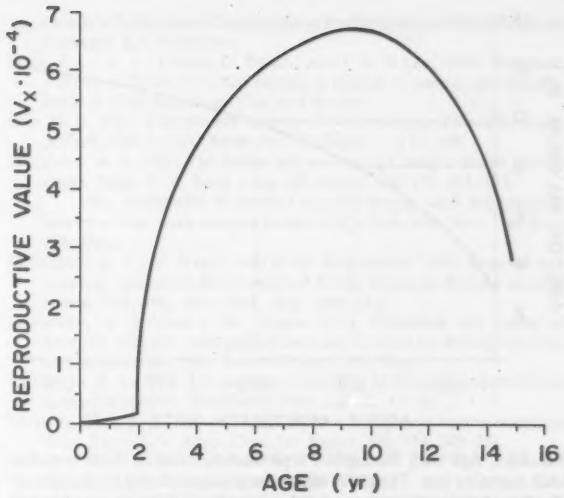

FIG. 9. Estimated reproductive value at each age for the Queen Charlotte Islands stock. The calculations assume knife-edge maturity at age 3 and an annual instantaneous mortality rate of 0.45 during the adult phase (Beverton 1963).

Using the average life history characteristics of the Queen Charlotte stock in 1974, I estimated that the maximum reproductive value occurs between age 9 and 10. In fact, a 9-yr-old herring can expect to produce 6.8×10^4 more offspring during its life span than a newborn individual (Fig. 9). This happens because in either a steady-state population where the adult mortality rate is high, or in an expanding population where r is positive, old individuals contribute more offspring to the next generation and therefore have the highest reproductive value. Conversely, the maximum shifts to a lower age whenever the adult mortality rate decreases, or when the population is declining (Fig. 10). Slobodkin (1963) observed that ages with the highest reproductive value are most sensitive to natural selection and hence are liable to rapid evolutionary change. Over the range of probable natural mortality rates ($0.3 < M < 0.5$), my calculations suggest that 8- to 10-yr-old herring have the highest reproductive value and therefore, traits that appear rather late in the life span should be under strong selection.

What then is the adaptive significance of the increase in egg size with age amongst the British Columbia stocks? For a fixed reproductive rate (recall that $m_x = R_x/2\theta_x$), any tendency to increase egg size will decrease m_x, which, in turn, will decrease the reproductive value and, most importantly, the fitness of the individual. This paradox vanishes if the ratio between the average egg weight of an age X female and a recruit spawner at age 3 (θ_3) is treated as a *minimum* estimate of offspring survival. For the Queen Charlotte stock, $\theta_3 = 0.00109$ g. Thus, presumably the survival value of an egg weighing θ_x grams cannot be less than $1/\theta_3$ or 917 times its weight. To put this into perspective, the eggs from a rather large, 220-g repeat spawner average 0.00152 g and therefore must enjoy at least a 30–40% higher chance of survival than the eggs produced by a recruit spawner, to maintain the fitness of the larger female. These figures give some idea of the nature of the problem, but unfortunately only hint at the selective pressures or trade-offs involved. Although arguments have been advanced to explain why herring egg size varies seasonally, apparently no one has speculated why it is advantageous for repeat spawners to

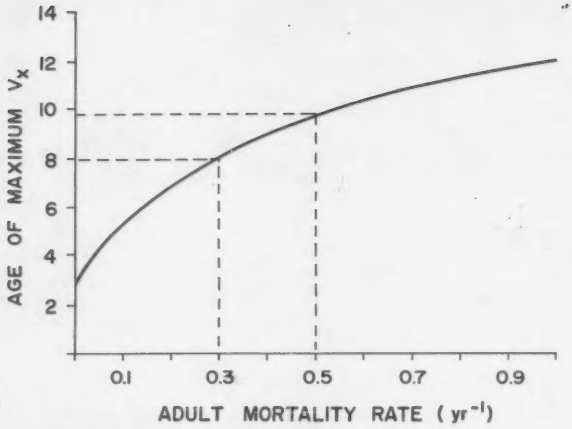

FIG. 10. Age with the highest reproductive value in relation to the adult mortality rate. The curve shown here is specifically for the Queen Charlotte Islands stock, but applies generally to the other stocks, for the same assumptions.

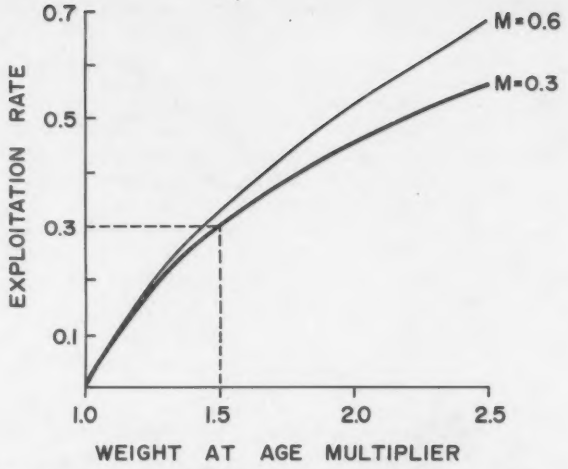

FIG. 11. Increase in body weight of adult herring required to produce the same number of eggs, at different exploitation rates, as the virgin stock. The curves indicate trajectories of equal egg production, where the ratio of exploited stock eggs/virgin stock eggs is equal to one, assuming constant recruitment and knife-edge maturity at age 3. The exploitation rate is defined as F/Z, where F is the instantaneous rate of fishing mortality, Z is the instantaneous total mortality rate ($Z = F + M$), and M is the natural mortality rate.

produce larger eggs than recruit spawners, when they both spawn at roughly the same time and place (Blaxter and Hunter 1982). In British Columbia there is a tendency for proportionally more recruit spawners to participate in the second spawning wave, which follows the first wave by about 2 wk (Hay 1985). Perhaps the planktonic food supply in this case changes during the spawning period, so it is advantageous for larvae from the later spawning to be smaller.

Resilience

Pacific and Atlantic herring exhibit some pervasive responses to overfishing and unfavorable environmental changes that tend to compensate for a decline in stock abundance. These responses have been well documented during the rise, and subsequent collapse, of three major fisheries. In the southern North Sea, herring growth rates (in weight) increased by at least 25%, and the age at first reproduction decreased by 2 yr as the fishery intensified. The net result is that the size at first reproduction has remained approximately constant (Murphy 1977). On the other side of the world, when the Hokkaido–Sakhalin stock was declining between 1940 and 1955, the average weight at age increased about 50% and the age at first reproduction fell from age 3 to age 2 (Motoda and Hirano 1963). Finally, in the Arcto–Norwegian stock, which collapsed in the late 1960s, the weight at age rose 50% between 1950 and 1973 (Dragesund et al. 1980). The Norwegians also observed that the age of maturity has varied, since the 1975 year class grew more slowly and matured later than the two preceeding year-classes, which grew extraordinarily fast and matured at 3 yr.

Thus, the fall in abundance of all three stocks set a chain of events in motion that increased the size at age and decreased the age at first reproduction. The obvious, and I believe correct, conclusion is that these changes were caused by population reduction, and perhaps secondarily by environmental change, genetic change, or some combination of these factors (Murphy 1977). In two of the three case histories examined it is of interest that the *maximum* increase in size at age was about 50%. This rule also seems to hold for the British Columbia stocks where the maximum increase in weight at age between the late 1930s and mid-1940s, when the stocks were buoyant, and 1971–75, when they were recovering from the minor collapse in the late 1960s, was of the order of 1.3–1.7 times.

To appreciate the implications of this response, I calculated the hypothetical egg production of the Queen Charlotte Islands population for different sizes at age and exploitation rates. The curves in Fig. 11 show the trajectories of equal egg production, equal, that is, to the virgin stock where the size at age multiplier is 1 and the exploitation rate is zero. Assuming knife edge maturity at age 3, and an exploitation rate (F/Z) of 0.3, the average female weight at each age would have to increase 1.5 times, relative to what it was in the virgin stock, for the exploited stock to produce the same number of eggs. Similarly, if the weight at age increased by a factor of 2 the stock could compensate for an exploitation rate of 0.4–0.5 depending on the natural mortality rate. Over the observed range of increase in the size at age the equilibrium exploitation rate is not particularly sensitive to the natural mortality rate (Fig. 11).

The foregoing analysis implies that the maximum growth response defines the ability of a population to stabilize itself in the face of random variations in recruitment. Cushing (1975) has argued that the more fecund gadid populations have a greater capacity for stabilizing themselves than the clupeids, and therefore, the gadids can tolerate greater exploitation rates. Between 1954 and 1967 the instantaneous fishing (F) and natural mortality (M) rates of British Columbia herring averaged 0.59 and 0.36, respectively (Schweigert and Hourston 1980). Thus, the exploitation rate was about 0.62, which is well beyond the compensatory capacity of the stocks. It is therefore not surprising that after a run of two or three poor year-classes in the 1960s, eight of the nine major herring populations declined sharply in abundance (Hourston 1980). Although my calculations are only approximate they suggest that if the maximum growth response is about 50%, then the British Columbia stocks should be able to sustain an exploitation rate between 0.2 and 0.3. At this level of harvesting the population should enjoy the

same prospects for recruitment as an unexploited stock with minimal risk of recruitment overfishing.

To sum up, experience has taught us that herring populations are not very stable. When growth conditions are favorable, particularly when the population is declining, the average weight at age can increase by as much as 50%, and the age at first maturity can decrease by 1 or 2 yr. If this is the maximum compensatory response, then Pacific herring can sustain an exploitation rate of about 0.3, which is similar to the conclusion reached by conventional stock assessment analyses (Environmental and Social Systems Analysis Ltd. 1982). Herring fishery managers should, therefore, opt for a conservative harvesting policy, and should not be swayed by the ability of the stocks to absorb high exploitation rates for one or two decades of generally favorable environmental conditions and above average recruitment, such as we observed in British Columbia in the 1940s and 1950s. Inevitably, conditions will take a turn for the worse, and when they do a conservative harvesting policy is more likely to see the stock weather a period of poor recruitment.

Acknowledgments

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Growth and Maturation of Pacific Herring (*Clupea harengus pallasi*) in the Strait of Georgia[1]

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Haist, V., and M. Stocker. 1985. Growth and maturation of Pacific herring (*Clupea harengus pallasi*) in the Strait of Georgia. Can. J. Fish. Aquat. Sci. 42(Suppl. 1): 138–146.

Juvenile growth rate, adult surplus energy, and the maturation schedule for the Strait of Georgia Pacific herring (*Clupea harengus pallasi*) stock were investigated over the period 1950–81. The variance in weight at age 2 is largely accounted for by juvenile abundance and sea surface temperature, indicating density-dependent juvenile growth moderated by environmental factors. Density and environmental factors have been equally important in moderating juvenile growth. Yearly variation in maturation of 3-yr-old herring is related to their average length; however, in two of the eight years studied the 3-yr-olds matured at considerably smaller sizes. The variance in adult surplus energy (growth plus gonad production) was largely accounted for by body weight, adult biomass, and sea surface temperature. A dome-shaped relationship between surplus energy and biomass was indicated, suggesting that over a broad range of population size, adult surplus energy is not density dependent. The relationship of sea surface temperature to both juvenile growth and adult surplus energy was quadratic with an optimum value. Recruitment biomass has been a relatively larger component than adult production of total stock growth, particularly during the period of high fishing intensity. This resulted in large fluctuations in stock biomass; in recent years, with lower fishing intensity, adult production has been a larger component of stock growth, and the stock biomass has become more stable.

Les auteurs ont étudié le taux de croissance des juvéniles, l'énergie supplémentaire chez les adultes et le calendrier de maturation du stock de hareng du Pacifique (*Clupea harengus pallasi*) du détroit de Géorgie pour la période 1950–1981. Ils expliquent la variance du poids à 2 ans en grande partie en termes de l'abondance des juvéniles et de la température superficielle de la mer, ce qui dénote une croissance des juvéniles dépendante de la densité et modérée par des facteurs environnementaux. Ces deux facteurs ont une part égale dans la modération de la croissance des juvéniles. La variation annuelle de la maturation chez les harengs de trois ans est reliée à leur longueur moyenne ; toutefois, en deux des huit années étudiées, ils sont devenus matures à des tailles considérablement plus petites. Le poids corporel, la biomasse des adultes et la température superficielle de la mer justifient en grande partie la variance de l'énergie supplémentaire (croissance plus production de gonades) chez les adultes. Selon la relation en dôme entre l'énergie supplémentaire et la biomasse, l'énergie supplémentaire chez les adultes ne dépend pas de la densité, quand on tient compte d'une vaste gamme de tailles de la population. Des relations quadratiques à valeur optimale étaient présentes entre, d'une part, la température superficielle de la mer et la croissance des juvéniles et, d'autre part, entre cette première variable et l'énergie supplémentaire chez les adultes. La biomasse au recrutement représentait une plus grande composante de la croissance totale du stock que la production d'adultes, surtout pendant la période de pêche intensive, ce qui entraînait de grandes fluctuations de la biomasse du stock. Au cours des dernières années, la production d'adultes est devenue une composante plus importante de la croissance du stock et la biomasse du stock est devenue plus stable à la suite d'une pêche moins intensive.

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Factors affecting growth rates can be of fundamental importance to the understanding of the dynamics of exploited fish populations. Changes in growth rates will directly affect stock productivity and can also indirectly affect the reproductive potential of the stock through shifts in age at maturity and individual reproductive output. As such, density-dependent growth will act to stabilize exploited populations; density-independent growth can have a destabilizing influence.

The evidence for density dependent growth in herring stocks is contradictory. Increased size at age has been observed in the Hokkaido stock (Motuda and Hirano 1963), the Arcto–Norwegian stock (Dragesund et al. 1980), and the southern North Sea stock (Murphy 1977) during periods of drastic stock decline. However, with the exception of these three stocks there is little evidence for density-dependent growth rates in post-recruit herring (Murphy 1977). There is considerable evidence for density-dependent juvenile growth; Sinclair et al. (1982)

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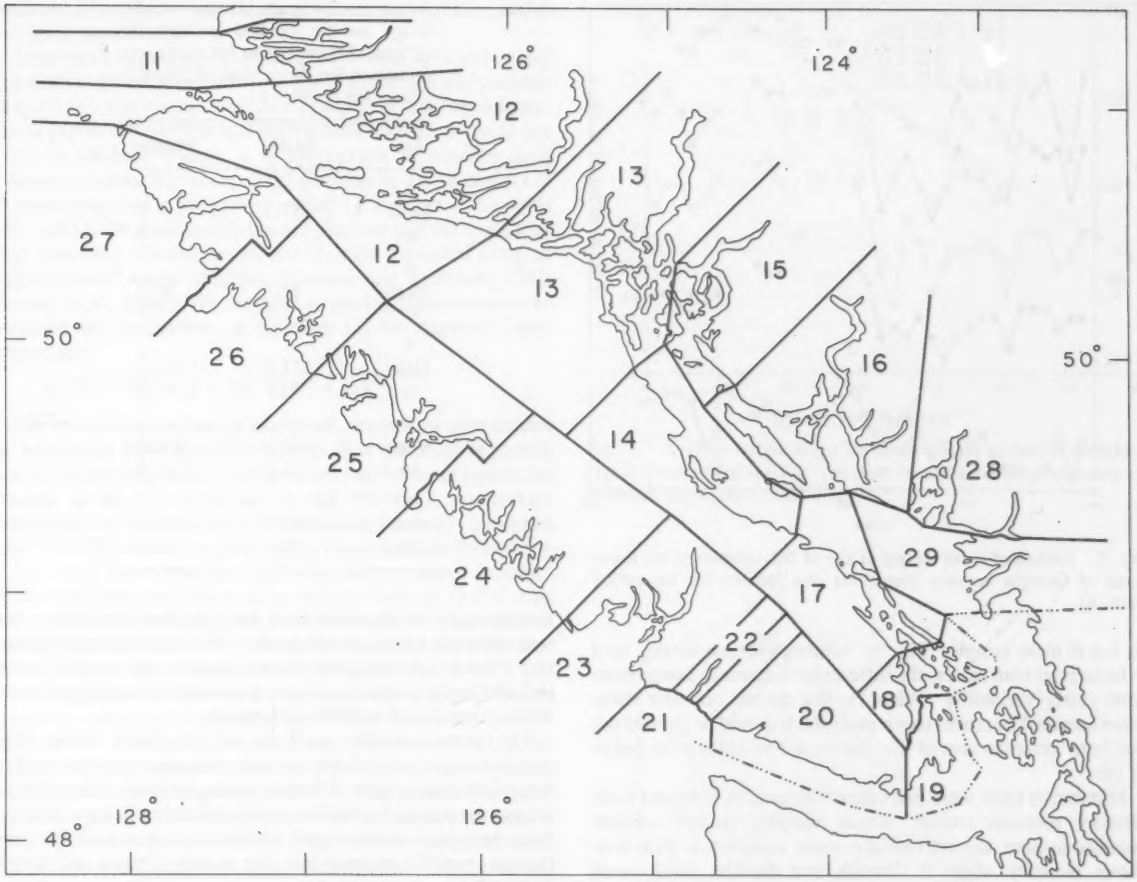

FIG. 1. Statistical areas in southern British Columbia.

discussed much of the literature. In fact, Lett and Kohler (1976) hypothesized that density-dependent growth in the 1st yr, and its subsequent effect on age at maturation and therefore population fecundity, has been an important mechanism for regulating the Gulf of St. Lawrence herring stock. This hypothesis is largely supported by an analysis of the northern North Sea stocks (Hubold 1978). Juvenile growth (l_1) was shown to be density dependent, subsequent length at age was related to l_1, and maturation was related to the average length of fish in a cohort. However, Moores and Winters (1982) found no evidence for density-dependent juvenile growth in the Fortune Bay herring stock, and their results indicated that l_1 is related to environmental conditions.

The British Columbia herring stocks have fluctuated dramatically over the past 30 yr and were all at severely depressed levels in the late 1960's. Hourston (1980) did not find evidence for an increase in length at any age in these stocks. In this study we reanalyze the data base for one of these stocks and attempt to discern the relative importance of density and environmental factors on growth rates. Blaxter and Hunter (1982) suggested that growth in length may reach a maximum at a relatively low feeding rate with L_∞ a more strictly controlled genetical characteristic than W_∞. We have therefore restricted the growth analysis to weight information. We also investigate the effect of size on maturity rates; however, for this analysis only length data are available. In the final section of this paper the relative importance of recruit and adult production to stock dynamics over the past 30 yr is investigated.

Methods

For this study of herring growth we have selected a migratory stock of Pacific herring (*Clupea harengus pallasi*) that resides in waters surrounding southern Vancouver Island. The adult stock moves offshore after spawning in the spring to feed on the continental shelf; in the fall, a reverse migration occurs and large schools congregate in the lower Strait of Georgia (statistical areas 17–19) from November until prior to spawning in early March. Although spawning stocks have not been clearly defined, this "stock" appears to spawn throughout statistical areas 14–19 (Fig. 1). Prior to 1970 a major winter reduction fishery occurred primarily in the lower Strait of Georgia. Since 1971 the major fisheries have been on spawning stocks throughout the Strait of Georgia. In addition, minor winter fisheries have taken place in the lower Strait.

Biological data used for the growth analysis were restricted to purse-seine caught samples obtained from November to January in statistical areas 17–19. Individual fish in the samples were not aged and weighed between 1965–70 so this period is not included in the analysis. We calculated mean weight at age for

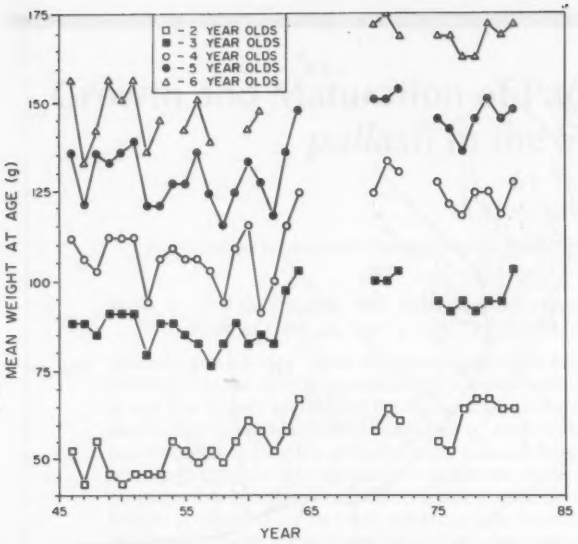

FIG. 2. Estimated mean weight at age of fish samples in the lower Strait of Georgia between November and January for the period 1946–81.

all fish in these samples (Fig. 2). Although female herring tend to be heavier than males, the difference is minor in comparison with yearly variability (Table 1). We do not consider these male/female differences in our analysis. It should be pointed out that "age" refers to year of life, that is, a 2-yr-old is in its 2nd yr of life.

Maturation rates were calculated for samples obtained from offshore research cruises. These samples, unlike samples obtained inshore, are not biased towards mature fish. Fish at or above maturity stage 3 (Parrish and Saville 1965) were considered mature; only samples obtained between October and December were used.

Abundance-at-age estimates have been obtained from a stock reconstruction using an age-structured model (Fournier and Archibald 1982). The model has been described elsewhere (Stocker et al. 1985). The estimates used for the Strait of Georgia and Johnstone Strait. Although this encompasses a larger area than considered for growth information, and possibly two or three stocks, we feel that the trends in abundance estimates will adequately reflect the densities affecting growth. Offshore distributions have not been well defined but it is probable that there is considerable overlap in the summer feeding areas utilized by different populations. Estimated numbers at age are for the postspawning population on July 1. Adult biomass was calculated as the sum of age 4 and older fish times the average weight at age during the preceding winter. Thus, we assume that the weight loss from reproduction (March) is regained by July 1, and increase in somatic weight occurs from July through the fall. July 1 is the theoretical "birthday" of British Columbia herring so that the 3-yr-old age class in December becomes the 4-yr-old age class on July 1.

Environmental factors investigated in this analysis are sea surface temperatures at Amphitrite Point and Kains Island (Hollister and Sandnes 1972; L. F. Giovando, Institute of Ocean Sciences, Sidney, B.C., pers. comm.), upwelling indices at 48°N, 125°W (Bakun 1973), and adjusted sea levels at Tofino (National Marine Fisheries Service, Monterey, CA). The

TABLE 1. Estimates of mean weight at age and the standard deviation of estimates between years for males and females in the lower Strait of Georgia (Nov.–Jan.), 1946–81.

Age	Males	Females
2		
Mean	57.3	55.9
SD	7.0	8.8
3		
Mean	88.1	91.5
SD	7.2	7.4
4		
Mean	111.4	113.9
SD	10.5	11.6
5		
Mean	134.2	138.3
SD	12.5	16.2
6		
Mean	154.7	156.0
SD	18.2	13.1

average value of these variables between April and September was evaluated in the growth models. When examining temperature effects both temperature and temperature squared were included in the models to allow a quadratic relationship between this environmental variable and growth.

The growth models used are all essentially linear after transformation, and a stepwise regression procedure was used to determine significance of independent variables. This method utilizes the partial F-criterion to determine significance. That is, the contribution made by each variable is evaluated as if it were the last variable entered into the model (Draper and Smith 1966). Because we are interested in evaluating the relative importance of density and environmental factors on growth we have also looked at the regression sum of squares for the independent variables using a forward regression procedure where variables are entered in the model in a specified order. The sum of squares estimate for each independent variable then represents the portion of variation of the dependent variable explained when entered in the model at that particular point.

Results

Juvenile Growth

For juvenile growth analysis, mean weight at age 2 was used as the growth variable. Growth throughout the first two summers of life is accounted for by this variable, and a growth response to density should be clearly evident it if exists. Environmental variables were evaluated for only the 2nd yr. Biological samples were obtained from inshore waters and they will be biased to the larger 2-yr-olds; some will mature that season. However, if factors influencing growth affect all fish in a cohort similarily, the trends in mean weight at age in these samples should reflect the entire year class.

The model we have used to describe growth to age 2 is

$$(1) \quad W = W_\infty e^{\delta N} e^{\gamma E} e^{\phi E^2}$$

where W is mean weight (grams) at age 2, N is "competing" population abundance, E is an environmental variable, E^2 is

included in the model only for temperature, and w_∞, δ, γ, and ϕ are fitted parameters.

Equation 1 implies that average growth for a particular cohort is a multiplicative, nonlinear function of maximum size possible at age 2 (w_∞), environmental factor, and year class abundance. Since part of the 3-yr-old age class school with the 2-yr-old age class in offshore waters, it is appropriate to consider both cohorts in estimating "competing" abundance. Two estimates of N were examined in the growth model: (1) number of 2-yr-olds (N_1) and (2) the number of 2-yr-olds plus one half the number of 3-yr-olds (N_2). Parameters N_1 and N_2 were estimated using an age-structured model analysis (Fournier and Archibald 1982; Stocker et al. 1985). We used the following transformation to estimate the parameters in equation (1) by stepwise linear regression:

$$\ln(W) = \ln(w_\infty) + \delta N + \gamma E + \phi E^2.$$

Of the environmental factors examined, sea surface temperature at Amphitrite Point provided the best fit in the juvenile growth model. Upwelling indices and sea level data were not significant factors in the growth model at the 5% level; sea surface temperature at Kains Island was significant; however, the model fit ($r^2 = 0.51$) was not as good as that for Amphitrite Point ($r^2 = 0.75$). Both the temperature and temperature squared variables were significant and indicated an optimal value at 12.2°C (that is, $\gamma > 0$, $\phi < 0$); temperature was included in the final model as the squared deviation from the optimum so that the parameter w_∞ represents the maximum size attainable at age 2.

The regression results show that N_2 provides a better fit to the observed variation in weight at age 2 than N_1 (Table 2, $r^2 = 0.75$ vs $r^2 = 0.67$). This supports our concept that the 3-yr-old cohort, through association with 2-yr-olds, is an important component of the "competing" density. Throughout the range of observed juvenile abundance this variable appears to have a major influence on juvenile size (Fig. 3). The estimated value for the parameter $\ln(w_\infty)$, 4.38, indicates that the theoretical maximum weight attainable by age 2 is approximately 80 g, or 15% greater than the maximum observed mean weight at age 2.

The relative effects of density and temperature at moderating juvenile growth are shown in the response surface (Fig. 4). Although there is no unique statistical test to discern the relative importance of variables in multiple regression analysis the relative contribution of each to the regression sums of squares provides an indication of their relative importance as predictors of growth. In this analysis the density variable (N_2) accounted for 55% and the environmental variable for 45% of the regression sum of squares when entered in the growth model in that order. When these variables were entered into the regression in reverse order, density still accounted for a greater proportion of the regression sums of squares (57%) than did temperature (43%), indicating density has been somewhat more important in moderating juvenile growth (Draper and Smith

TABLE 2. Analysis of variance table for multiple regression of juvenile growth model where independent variables were entered in a specified order. SS_1 is the sum of squares when density is entered first, SS_2 when the environmental variable is entered into the regression model first. The environmental factor is the squared deviation from the optimal mean summer sea surface temperature of 12.2°C. Calculated F values are from the SS_2 regression.

Source of variation	df	SS_1	SS_2	F value	Prob. (F-tail)
Total	25	0.4403			
Regression	2	0.3282		33.65	0.0000
Density (N_2)	1	0.1808	0.1883	38.62	0.0000
Environment (E)	1	0.1473	0.1399	30.22	0.0000
Residual	23	0.1121			
Equation $\ln(W) = 4.367 - 0.0014(N_2) - 0.0926(E)$, $r^2 = 0.75$					
Total	25	0.4403			
Regression	2	0.2928		22.82	0.0000
Density (N_1)	1	0.1515	0.1529	23.84	0.0001
Environment (E)	1	0.1413	0.1399	22.03	0.0001
Residual	23	0.1475			
Equation $\ln(W) = 4.306 - 0.0014(N_1) - 0.0907(E)$, $r^2 = 0.67$					

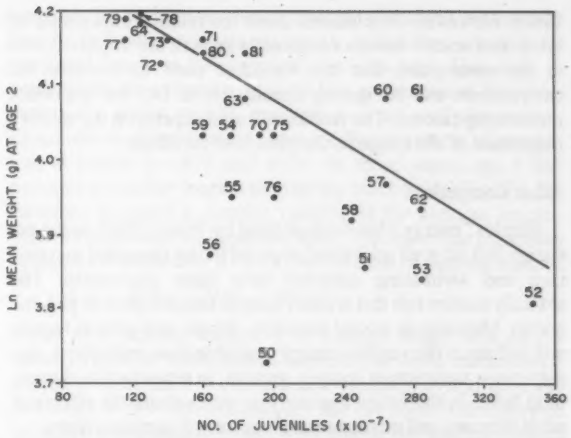

FIG. 3. Average weight at age 2 in relation to the number of juveniles (age 2 + one half of age 3's). The solid line indicates the relationship at optimum temperature (12.2°C).

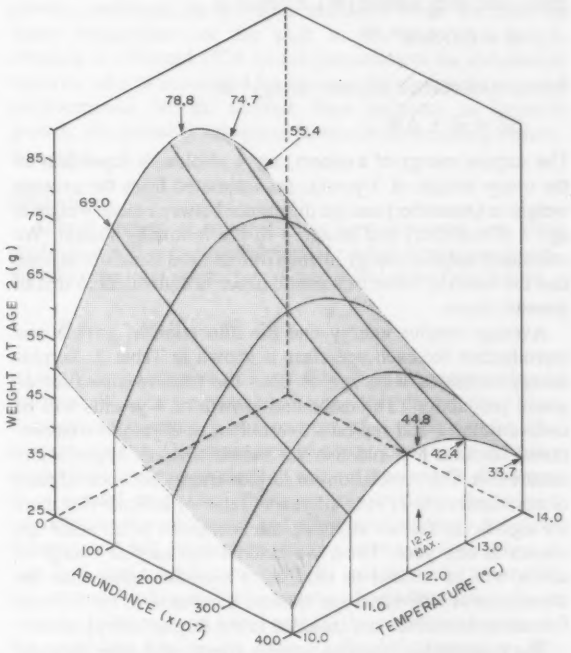

FIG. 4. Response surface for weight at age 2 in relation to juvenile abundance and temperature.

1966). However, conclusions about the relative importance of biotic and abiotic factors on juvenile growth are implicitly tied to the assumption that the variables used to describe the environment and competing density are in fact the important moderating factors. The results will also depend on the relative magnitude of the range in the observed variables.

Adult Energetics

Surplus "energy" has been defined by Ware (1980) as the net energy left after all additional costs of living (standard metabolism and swimming activity) have been discounted. For sexually mature fish this is equivalent to somatic growth plus the energy liberated as sexual products. Biotic and abiotic factors will influence the surplus energy available to an individual; this may cause variation in somatic growth, in reproductive output, or in both. In the following analysis we evaluate the effects of adult biomass and environmental factors on surplus energy.

Ware (1985) has shown that the reproductive output of Pacific herring is dependent only on body weight; population size and environmental variability do not appear to affect gonad weight. The relationship he determined between ovary weight (R) in grams and body weight (W) in grams is

$$R = 0.098\, W^{1.208}.$$

We have calculated surplus "energy" as

$$SE = R + \Delta W.$$

The surplus energy of a cohort, say 4-yr-olds, is dependent on the ovary weight of 3-yr-olds (as estimated from the average weight in December) and the difference between mean weight at age 3 (December) and at age 4 in the following season. We calculated surplus energy in units of mass and therefore assume that the calorific value of somatic tissue is equivalent to that of gonadal tissue.

Average surplus energy and the allocation to growth and reproduction for each age class is shown in Table 3. Surplus energy increases with age as does the relative allocation to gonad production. The estimated growth of 4-yr-olds will be underestimated and reproductive output of 3-yr-olds overestimated because 3-yr-old fish are biased towards larger, more mature fish. The correlations of surplus energy between all pairs of age classes (4–7) over all years (Table 4) indicate that there are significant factors affecting the energetics of all adult age classes in any year. Thus, we assume that surplus energy of adults will be related to total adult biomass rather than the abundance of individual age classes. Sample sizes for 7-yr-old fish are small and are not included in the surplus energy model.

The relationship between surplus energy and adult biomass (Fig. 5) appears to be an asymptotic or dome-shaped relationship. Clearly, over the lower range of observed biomass, growth is positively related to adult abundance. To account for differences in initial body weight we assume that surplus energy is an allometric function of body size. Parker and Larkin (1959) and Ware (1978) have demonstrated that the form of relationship between somatic growth rate and body weight for semelparous species and immature fish is

$$dW/dT = \alpha W^{\beta}.$$

Growth studies suggest that environmental variability will affect the proportionality constant α, while β measures the complex of physiological processes underlying growth (Parker and Larkin 1959; Paloheimo and Dickie 1966). It is consistent

TABLE 3. Average surplus energy and the allocation to gonad weight, and growth for ages 4–7.

	Age			
	4	5	6	7
Growth (g)	23.7	23.0	18.8	15.4
Gonad weight (g for age −1)	22.1	29.3	37.8	48.2
Surplus energy (g)	45.8	52.3	56.6	63.6
Gonad weight/surplus energy	0.48	0.56	0.67	0.76

TABLE 4. Correlations between surplus energy for age classes 4–7 over all years. *Significant at the 0.05 level.

	Age		
Age	4	5	6
5	0.78*		
6	0.62*	0.62*	
7	−0.18	0.10	0.46*

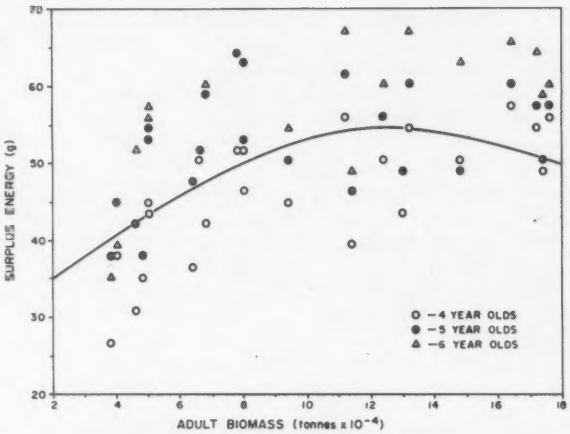

FIG. 5. Estimated surplus energy for ages 4–6 in relation to adult biomass (ages 4+) in the middle of the growth period (July 1). The solid line represents the predicted relationship (equation 2) for a 100-g fish.

with these observations to formulate our surplus energy model as

$$(2)\quad SE = \alpha W^{\beta} e^{\psi B} e^{\omega B^2}$$

where B is adult biomass and α, β, ψ, and ω are fitted parameters. The squared value of the biomass term is included to allow a dome-shaped response to this variable. Multiple regression was performed on the log transformed equation

$$\ln (SE) = \ln (\alpha) + \beta \ln (W) + \psi B + \omega B^2.$$

The regression results (Table 5) indicate that all variables in the model are highly significant. Initial weight accounted for 29% of the variation in the surplus energy estimates. Including a quadratic form for biomass increased the total variation explained by the relationship to 56%. Because reproductive output is calculated as a function of body weight it is not surprising that

TABLE 5. Analysis of variance table for stepwise regression of adult surplus energy models.

Source of variation	df	SS	F value	Prob. (F-tail)
Total	62	2.3734		
Regression				
Weight	1	0.7021	25.62	0.0000
Residual	61	1.6713		
Equation ln (SE) = 1.3468 + 0.548 ln (W), $r^2 = 0.29$				
Total	62	2.3734		
Regression	3	1.3377	25.40	0.0000
Weight	1	0.4927	28.07	0.0000
Biomass (B)	1	0.3707	21.12	0.0000
Biomass (B^2)	1	0.2604	14.83	0.0003
Residual	59	1.0375		
Equation ln (SE) = 1.1275 + 0.4865 ln (W) + 0.0980(B) − 0.0038(B^2), $r^2 = 0.56$				
Total	62	2.3734		
Regression	4	1.6084	30.49	0.0000
Weight	1	0.5381	40.80	0.0000
Biomass (B)	1	0.3001	22.75	0.0000
Biomass (B^2)	1	0.2224	16.86	0.0001
Environment (E)	1	0.2706	20.52	0.0000
Residual	58	0.7650		
Equation ln (SE) = 1.1468 + 0.5095 ln (W) + 0.0887B − 0.0036B^2 − 0.2002E, $r^2 = 0.68$				

weight is a significant factor in the surplus energy model. However, the point of interest is that a significant proportion of the residual variation in surplus energy, not accounted for by weight, is explained by the adult stock biomass. Both the biomass and biomass squared terms are highly significant, indicating a dome-shaped response ($\psi > 0$, $\omega < 0$) with maximum surplus energy at an adult biomass of 130 000 t.

Environmental factors were included in the surplus energy model by adding an additional multiplicative term to equation 2, that is

$$SE = \alpha W^{\beta} e^{\psi B} e^{\omega B^2} e^{\lambda E}$$

where E is the value of an environmental factor. Of the environmental factors evaluated, sea surface temperature at Kains Island produced the greatest improvement in the model fit. Upwelling, sea level, and sea surface temperature at Amphitrite Point were not significant factors at the 5% level. As in the juvenile growth analysis, sea surface temperature at Kains Island had an optimum value (11.4°C). Temperature was included in the final model (Table 5) as the squared deviation from the optimal value. Multiple regression results indicate that 68% of the variation in adult surplus energy is accounted for by body weight, biomass, and temperature.

Maturation Rate of 3-Yr-Old Herring

Samples obtained in offshore waters indicate a separation of herring by age; juvenile schools consist primarily of 2- and 3-yr-old fish and adult schools consist of age 3 and older fish. Average length and maturity rates of 3-yr-old fish in each school type (Table 6) indicate larger fish and higher maturity rates in adult schools. We have therefore not combined the data for the two schools in the following analysis.

There is a positive relationship between proportion mature and average size in each year and school type (Fig. 6). Regression analysis on these data indicates that 64% of the variation in proportion mature can be explained by average length. To further evaluate the length–maturation schedule we estimated length at 50% maturity for each year. However, in years where an extremely high or low proportion of fish were mature the length at 50% maturity was not well determined. Examination of the data did show a different pattern of maturation at length in 1972 and 1974. In these years, age 3 fish matured at smaller lengths than in the other years (Fig. 7). We therefore included a dummy variable in the average length–maturity regression for these two years. The following regression equation accounted for 91% of the variation in percent mature:

$$M = -305 + 1.97L + 26.0D$$

where M is percent mature, L is average length, and D is a dummy variable. These results indicate that while maturation is related to size, there is considerable variation over time in the size range over which fish mature. The two cohorts that showed increased maturation at length were among the smallest cohorts for the years in which maturity data are available; only the 3-yr-old cohort in 1980 was smaller. The average weight at age 3 in the spring roe fishery was also greater for these two cohorts, indicating that they may have experienced more favourable growth conditions the previous summer. While we have no direct explanation for the shift in the maturation–length schedule in 1972 and 1974, a high proportion of the variation in maturity rates is accounted for by size. Population density and environmental factors, through their influence on juvenile growth, are probably important factors in determining maturation rates.

Production

Annual growth of the stock has been separated into adult production and recruitment biomass. Adult production is estimated as the total production of age 4 and older fish, that is

$$P = \sum_{i=4}^{10} N_i(W_i - W_{i-1})$$

where N_i is the number of age i fish, W_i is the weight of age i fish, and W_{i-1} is the weight of age i fish the previous year. Recruitment biomass is the number of 3-yr-olds times their average weight. Our estimates of stock growth are therefore equivalent to surplus production without the removal of biomass from natural mortality. Thus, we can evaluate the relative importance of recruitment and adult production to the stock dynamics. Adult production, recruit biomass, stock biomass (age 3+), and catch for the 1950–81 seasons (July 1–June 30) are presented in Fig. 8. Two estimates of population biomass are shown: (1) biomass on July 1 and (2) the remaining biomass of the same age classes on June 30 the following year. The difference between the July 1 and June 30 biomass estimates is the result of a decrease in biomass from fishing and natural mortality, and an increase in biomass from adult production. Recruits are added to the June 30 biomass in one season to give the July 1 estimate of biomass the following season.

During the period 1950–67, catches were high and the population fluctuated rapidly. Recruitment biomass was a large component of the July 1 biomass and subsequent catch. The fishery was basically not regulated and catches were closely related to total biomass. Three poor year classes, recruiting between 1965–67, caused the population to decline to such low levels that the reduction fishery was closed. The stock recovered quickly with minimum fishing pressure, and since the inception of a roe fishery in 1971 catches have been regulated at relatively

TABLE 6. Average length, percent mature, and number of 3-yr-olds for offshore juvenile and adult samples.

School type	Year							
	1969	1970	1971	1972	1974	1975	1976	1980
Juvenile schools								
Avg. length (mm)	184.6	181.0	181.1	183.2	184.0		173.1	169.8
% mature	70.8	61.2	39.8	85.5	87.5		40.8	25.2
No. of fish	374	278	289	173	239		147	210
Adult schools								
Avg. length (mm)	199.9			193.1	189.4	190.2	183.9	184.9
% mature	92.0			98.6	91.4	64.7	48.2	65.0
No. of fish	162			428	140	34	56	457

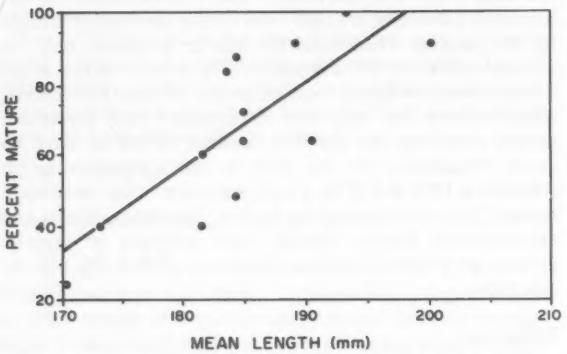

FIG. 6. Percent mature in relation to average length of 3-yr-olds in offshore samples. The solid line represents the least squares regression fit.

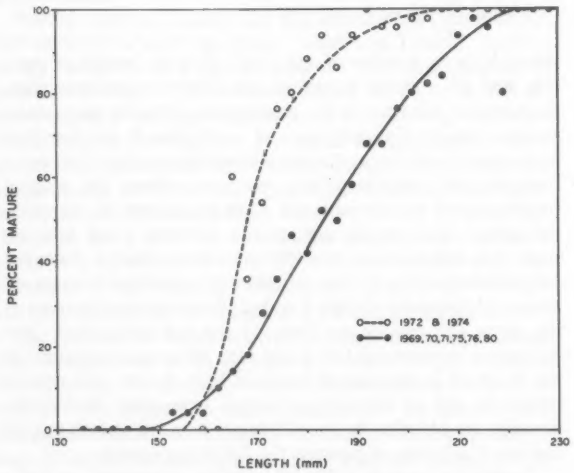

FIG. 7. Proportion of fish mature in relation to length group (3-cm intervals) for two time periods. The curves are fitted by hand.

low levels. The stock biomass has been relatively stable in the past 10 yr; recruitment biomass has been generally lower than during the reduction fishery period (see also Stocker et al. 1985). The important observation here is that through the period of high fishing intensity (1950–68) when the major component of the stock was the recruiting year class the stock fluctuated

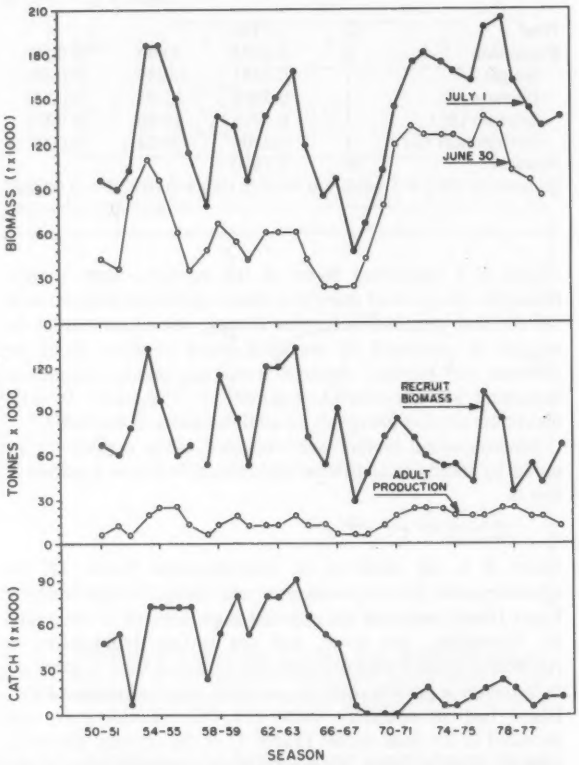

FIG. 8. Temporal trends in biomass (ages 3+), production, and catch for the Strait of Georgia herring stock.

erratically over short time periods. Since the inception of the roe fishery (1971), and much reduced catch levels, recruits have been a lesser component of total stock production and the stock has become much more stable.

Discussion

This study supports the hypothesis that juvenile growth is density dependent, a result that is consistent with numerous studies of juvenile fish growth. Ware (1980) summarized much of the literature on density-dependent growth of juvenile pelagic fish and Iles (1967), Anthony (1971), Lett and Kohler (1976),

and Hubold (1978) demonstrated density-dependent growth in juvenile herring stocks specifically. Moores and Winters (1982) found that juvenile growth in Fortune Bay herring was related to environmental conditions and was independent of cohort size; Iles (1973) demonstrated an interaction of both density and environment affecting growth of juvenile sardines. Our study also showed environmental variation (mean sea surface temperature) to be an important factor in moderating growth to age 2. The results indicate that juvenile abundance and temperature have been about equally important in their effect on juvenile growth in the lower Strait of Georgia population.

Our analysis of adult energetics indicates a dome-shaped relationship between surplus energy and adult biomass. This result is counterintuitive: a hypothesis based on ecological principles would suggest that the food available to an individual, if limiting, should be inversely related to biomass and therefore surplus energy should be inversely related to the adult biomass. The surplus energy estimates are dependent on the assumption that reproductive output is strictly a function of body weight. However, if reproductive output increases at low biomass levels a reasonable alternative hypothesis would be that surplus energy is independent of biomass. The work of Ware (1985) supports the assumption that reproductive output is independent of density. It should be pointed out that Ware's relationship between ovary weight and body size is based on 3 yr of data obtained over all British Columbia herring stocks. At least one of these stocks (the north coast) appears to have been at very depressed levels during this period (Stocker et al. 1983) but did not show a significant change in reproductive output. Another line of support for the assumption that gonad production is independent of density and environmental variation comes from impoundment studies of adult British Columbia herring. Brett and Solmie (1982) found that feeding impounded herring from January until spawning in April did not alter gonad weights, although body weight was higher in fed fish. Thus, although we cannot eliminate the possibility of increased reproductive output at low densities, we feel there is currently no evidence to support this concept for British Columbia herring.

Density-dependent growth of adult herring has only shown up clearly in stocks when their abundance was drastically reduced. The Strait of Georgia herring stock was at its lowest levels from 1965 to 1969, a period for which weight at age data are not available. However, weights at ages 3–6 were higher in 1970–72 than they had ever been (Fig. 2), and these cohorts were born, and grew up, when the stock was at its lowest recorded levels. It is not possible to ascertain if this increased size at age is the result of increased juvenile or adult growth; therefore, we cannot eliminate the possibility of density-dependent adult growth for this herring stock.

A positive relationship between growth rate of adult herring and cohort size has been shown for the southwest Nova Scotia herring stock (Sinlair et al. 1982). They proposed a mechanism for this relation based on schooling fish in a patchy environment. They suggested that at increasing population density the overall food abundance, which would have to be nonlimiting, is more efficiently located, that is, more patches of food per day are found when schools are larger. This assumes that there are behavioural mechanisms involved in schooling such that information on location of food patches is passed between individuals, and that the benefits gained by locating more food patches are not outweighed by less food available per individual in larger schools. We do not have an alternative mechanism that would produce a positive relationship between surplus energy and density below optimal levels.

The value of the weight-exponent β in the surplus energy model was found to be approximately 0.5. Ware (1978) has suggested that for pelagic fish this exponent should range from 0.7 to 0.8 based on considerations of optimal foraging and the cost of acquiring energy. However, he suggested that this exponent may be <0.7, depending on the size and concentration of prey normally encountered. Parker and Larkin (1959) indicated that growth rate may increase proportionally to body weight because a number of physiological rates appear to be proportional to weight to a fractional exponent, and they suggested that standard metabolic rate may be directly proportional to growth rates. They found that the exponent for growth varied between 0.56 and 0.80 for two species. The low weight exponent determined in this analysis may result from our assumption that the energy content of gonadal tissue is equivalent to that of somatic tissue. McGurk et al. (1980) found in Atlantic herring (*Clupea harengus harengus*) prior to spawning that the calorific value of ovary tissue was approximately 1.2 times the value of somatic tissues. The energy contents of different tissues have not been determined for Pacific herring; however, they are likely to be similar to those of Atlantic herring.

An interesting outcome of our analysis is the result that sea surface temperature has an optimum value for both juvenile growth and adult surplus energy. Ecological studies that have examined the effect of temperature, as an environmental variable, on growth have generally found a positive relationship over the range of observed temperatures (e.g. Moores and Winters 1982; LeCren 1958). Bakun and Parrish (1980) indicated that perhaps the most important reason sea surface temperature is commonly used as an environmental variable in studies of biological variation is because biological processes increase and decrease with temperature. They also stated that temperature provides a signal of important ocean processes. Physiological studies support the concept that fish growth is maximum at some optimal level. Brett's (1976) review of the literature cites optimal temperatures for a number of species. Optimal temperatures for herring growth do not appear in the literature. However, Brett (1976) showed that the optimal temperature for growth of salmonids and yellowtail flounder (*Limanda ferruginea*) corresponds closely to average summer temperature in their natural habitat. If we extrapolate this result to herring we would conclude that the observed dome-shaped relationship between growth or surplus energy and temperature results from a direct physiological effect. Alternatively, the observed relationship could also result from temperature effects on the relative abundance of prey species, or temperature may just be an indicator of other oceanic factors (e.g. upwelling).

An increase in maturation rate (percent mature at age) resulting from accelerated growth has been documented for a number of herring stocks (Hubold 1978; Moores and Winters 1982; Winters 1976; Lett and Kohler 1976). In this study we found similar results; however, maturation was not entirely dependent on the average length of fish in a cohort. In two of the eight years studied, fish were mature at considerably smaller lengths than in the other years. Sinclair et al. (1982) found significant shifts in length at 50% maturity that appear to be related to cohort density.

Our results indicate that density-dependent juvenile growth and its subsequent effect on age at maturation will to some extent stabilize recruitment. However, this mechanism will be

limited in its ability to regulate the population because of significant environmental effects on growth, and possibly maturation. Large variation in recruitment biomass, the major component of total stock production, has resulted in erratic stock fluctuations over the past 30 yr. These fluctuations have been largely dampened in recent years, a period of reduced fishing intensity. However, the reason for the relative stability of stock biomass since 1970 is not well determined. That is, recruitment has been generally lower and less variable, and adult production has been a larger component of total stock production. This may suggest that at high stock levels lower recruitment may be an important aspect of stock dynamics.

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Session 4: Clupeoid Production and Recruitment Models

An Investigation of the Population Dynamics of Atlantic Menhaden (*Brevoortia tyrannus*)[1]

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Reish, R. L., R. B. Deriso, D. Ruppert, and R. J. Carroll. 1985. An investigation of the population dynamics of Atlantic menhaden (*Brevoortia tyrannus*). Can. J. Fish. Aquat. Sci. 42(Suppl. 1): 147–157.

The following biological components concerning the population dynamics of Atlantic menhaden (*Brevoortia tyrannus*) were investigated: growth, natural mortality, migration, fishing mortality, and recruitment. We found that a hypothesis of density-dependent growth is strongly supported by the data and that the dependence of growth on abundance appears to occur prior to recruitment. Age-specific natural mortality estimates seem biologically reasonable, except the estimate for age 1 menhaden, which appears to be too low. Most of the estimated migration probabilities also seem to be biologically reasonable, especially during the summer season for age 2 fish. Estimated age-specific fishing mortality rates demonstrate the increased fishing pressure on age 3 and younger fish since the early 1960's. When the environmental variables (temperature and Ekman transport) are excluded from the spawner–recruit analysis, then the Beverton–Holt model fits as well as other models examined, and it is the only model that is significant at the 0.05 probability level. Of the environmental variables examined, only westward Ekman transport in the South Atlantic region shows a relationship with recruitment. The unnormalized gamma function, which includes the Ricker model as a special case, is more responsive to the inclusion of westward Ekman transport than the Beverton–Holt model.

Notre étude a porté sur les composantes biologiques suivantes de la dynamique des populations de l'alose tyran (*Brevoortia tyrannus*) : croissance, mortalité naturelle, migration, mortalité due à la pêche et recrutement. Nous avons trouvé qu'une hypothèse voulant que la croissance soit fonction de la densité était fortement appuyée par les données et que la dépendance de la croissance envers l'abondance se manifestait avant le recrutement. À l'exception de l'estimation pour l'âge 1 qui semble trop faible, les estimations de mortalité naturelle selon l'âge semblent acceptables du point de vue biologique. Il en va de même pour la plupart des estimations de probabilités de migration, surtout pour les poissons d'âge 2 au cours de l'été. Les taux de mortalité estimés spécifiques à l'âge 3 et moins de puis le début des années 1960. L'exclusion des variables environnementales (température et transport d'Ekman) de l'analyse frai–recrutement permet au modèle Beverton–Holt de s'ajuster aussi bien que les autres modèles étudiés ; ce modèle est le seul qui soit significatif au niveau de probabilité de 0,5. Des variables environnementales étudiées, seul le transport d'Ekman en direction ouest de l'Atlantique sud présente une relation avec le recrutement. La fonction gamma non normalisée, dont le modèle de Ricker est un cas particulier, est mieux adaptée à l'inclusion du transport d'Ekman en direction ouest que le modèle de Beverton–Holt.

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Because of rapid declines in the abundance of Atlantic menhaden (*Brevoortia tyrannus*) and because menhaden (Atlantic and Gulf) support the largest United States commercial fishery in terms of pounds landed, the need for a biological simulation model specifically designed for Atlantic menhaden was recognized. Because of this need, we were granted a contract by the National Marine Fisheries Services, and the first phase of that research was an overall investigation of the population dynamics of Atlantic menhaden. This paper highlights results of the first phase of research, which is presented in Deriso et al. (1983). Results of the second phase are reported in Ruppert et al. (1983).

We investigated the following biological components that were necessary for characterizing the population dynamics of Atlantic menhaden: growth, natural mortality, migration, fishing mortality, and recruitment. These components were later compiled into a stochastic simulation model for Atlantic menhaden. The realism of this model hinges to a large extent on the ability to estimate the parameters describing these components.

Growth rates of Atlantic menhaden vary in different fishing areas as well as from year to year. Fish caught in the North Atlantic are not only older, but larger for a given age than fish caught in the South Atlantic (Nicholson 1972). Atlantic menhaden, which can normally live to be 8 yr old, are relatively fast growing until at least age 4 at which time growth slows down (Henry 1971). From 1964 until the early 1970's, fish 4 yr and older had practically disappeared from the catch samples (Nicholson 1975). Nicholson (1971) attributed this decline in age structure and abundance to increased fishing pressure. During this same time period significant increases in growth rates have occurred over those in the late 1950's and early 1960's (Nicholson 1975). Nicholson (1975) concluded that these age-specific increases in length and weight are the result of the decrease in the average age of the menhaden stock.

Predators, parasites, and fluctuating environmental conditions are thought to be the most important factors contributing to natural mortality in Atlantic menhaden. Bluefish, *Pomatomus saltatrix* (Goode 1879; Ellison 1951; Bigelow and Schroeder 1953; Grant 1962), striped bass, *Morone saxatilis* (Merriman 1937; Hollis 1952), bluefin tuna, *Thunnus thynnus* (Crane 1936), and sharks (Field 1907; Bigelow and Schroeder 1953) are the primary fishes that prey upon Atlantic menhaden. Parasites of Atlantic menhaden range from copepods, which occur on the body surface and gills (Wilson 1932), trematodes, which reside on the gills and in the intestines (McMahon 1963; Linton 1905), isopods, which make use of the buccal cavity (Richardson 1905; Kroger and Guthrie 1972), to sporozoans, which are found in the testes (Hardcastle 1944). Reintjes (1969) also reported mortality in Atlantic menhaden caused by natural temperature extremes.

Recruited Atlantic menhaden are schooling pelagic oceanodromous fishes that migrate northward as waters warm in the spring and southward as waters cool in the fall (Lagler et al. 1977). Because of these migration patterns, the fishing season along the Atlantic coast varies in accordance with the seasonal arrival of menhaden schools. Fishing usually begins in April or early May south of Cape Hatteras, North Carolina, and by late May or early June, it will have extended to the North Atlantic (June and Reintjes 1976). The fishing season had formerly ceased by mid-October, but with improvement of larger and faster vessels, the season since 1963 extends at least into November (Nicholson 1971). June and Reintjes (1976) reported that the fishery in the South Atlantic (south of Cape Henry, Virginia) is most productive in May or June whereas the Chesapeake Bay and regions north are most productive in July or August. Most of the fall fishing occurs off the North Carolina coast from Cape Hatteras to Cape Fear during November and December. This temporal fishery is commonly referred to as the North Carolina fall fishery.

The annual catch for regions north of Cape Charles, Maryland, prior to 1963 amounted to 65% of the total catch, but after 1966 only accounted for less than 4% of the total catch (Nicholson 1975). The absence of older and larger menhaden, which comprise the majority of the catches in these northern regions, reflects a dramatic decrease in the number of older fish in the population. From 1955 through 1968 the average age of the catch in these northern regions was 3-yr-old menhaden whereas the bulk of the catch in the southern regions during this same period was made up of primarily age 1 and 2 menhaden (Henry 1971). Prior to the mid-1960's the bulk of the catch was mainly age 3+ fish, but since the mid-1960's about 90% of the total catch consists of fish less than age 3.

Atlantic menhaden are prolific spawners that reach maturity usually in three growing seasons. Menhaden appear to spawn wherever they happen to be when their ovaries ripen (Nicholson 1972). Spawning occurs every month from May to October off the North Atlantic shore. Spawning also occurs in March and April and also in September and October off the mid-Atlantic shore and from November through March off the South Atlantic shore (Higham and Nicholson 1964). During the winter spawning months, mixing of menhaden of all areas and ages are thought to occur south of Cape Hatteras (Nicholson 1972). Based on larval collections, Reintjes (1969) hypothesized that much of the spawning takes place in the winter months south of Cape Hatteras. Eggs and larvae, which are spawned in the open ocean, depend on Ekman, ocean, and tidal currents for transport to estuaries where they grow and develop before entering the recruited population offshore (Nicholson 1972; Nelson et al. 1977).

Growth Analyses

We analyzed data on area, age, and season-specific average monthly measurements of the length and weight of menhaden subsampled from commercial catches. These data were grouped into three seasons, March–May, June–August, and September–February, to take advantage of differences in regional stratification due to migration. The fishing areas north of Cape Charles and those including Cape Charles south were combined to form northern and southern areas, respectively. Also, we stratified this 1965–78 data base into three groups of years, 1976–78, 1970 and 1972–75, and 1965–69, which were years of high, medium, and low total abundance, respectively. We could not clearly define the abundance for 1971 as being either in the medium or low abundance class and therefore did not include the weights and lengths for 1971 in the analysis. The yearly age-specific abundances calculated using cohort analysis are presented in Deriso et al. (1983).

The following four basic questions are of interest: (1) How does mean length depend upon abundance, age, area, and season? (2) How does mean weight depend upon abundance, age, area, and season? (3) How does the relationship between weight and length depend upon abundance, age, area, and season? (4) How do growth rates depend upon abundance, age, area, and season?

We addressed question 1 by applying a factorial analysis of variance to logarithm of length (dependent variable) and abundance, age, area, and season as factors. We addressed question 2 with a similar analysis on the logarithm of weight. In both cases the logarithm transformation was applied because untransformed biological growth data usually exhibit two violations of the assumptions of analysis of variance: heteroscedasticity and a positively skewed error distribution. We examined residuals versus predicted values plots and normality plots of the residuals for both the log-transformed length and the log-transformed weight data. These plots indicate that the log-transformed data fit the assumptions of homoscedasticity and normally distributed errors. In both cases, F-tests show all four factors, abundance, age, area, and season, to be highly significant (Tables 1 and 2). For each level of a factor, the parameter in the table is the difference in the mean of the dependent variable between that level of the factor and the last level of the factor, with all other factors held constant. For example, the difference in the mean of $\log_e$ (weight) between high abundance years and the medium abundance years is estimated as -0.365. The estimated difference in the mean of $\log_e$ (weight) between low abundance years and medium abundance years is 0.184. The parameters are defined in such a way that the parameter for the last level of any factor must be 0. Therefore, it need not be estimated and has no standard error.

We found that length and weight increase with age and season and that northern fish tend to be larger than southern fish of the same age. Our results support the hypothesis that within an age-class northern fish tend to be larger than southern fish and are consistent with observations reported elsewhere (Nicholson and Higham 1964a, 1964b, 1965; Henry 1971; Nicholson 1975). We also found that both length and weight increase as abundance decreases. However, these analyses do not show at what age, or ages, this apparent dependence of growth on abundance occurs.

Besides the models reported here, we analyzed models containing interactions between the factors. In all cases, the magnitudes of the estimated interaction parameters are quite small. However, they are statistically significant (though much less significant than the main effects), but that is not unexpected considering the very large number of observations (898).

We addressed question 3 by analyzing a factorial design with the dependent variable $\log_e$ (weight) and the factors abundance, age, area, and season and a covariant $\log_e$ (length). We also included interactions between $\log_e$ (length) and each of the factors. Because length has been log-transformed, exponentials of the main effects together with the intercept serve as the scaling parameter (a), and the interactions with $\log_e$ (length) serve as the power parameter (b) in the relationship weight = $a \cdot \text{length}^b$. The interaction between $\log_e$ (length) and a particular factor measures the variation between levels of the factor in the slope of the regression of $\log_e$ (weight) on $\log_e$ (length). If this slope is 3, then menhaden growth is isometric; otherwise, growth is allometric.

The analysis is presented in Table 3. To find the estimated slope at a particular abundance, age, season, and area, one adds the estimated parameter for $\log_e$ (length), i.e. 2.881, to the estimated interaction parameters at that abundance, age, season, and area. For example, estimated slope for age 2 northern fish during the spring of a year of high abundance is $2.881 + 0.076 + 0.137 + 0.001 + 0.058 = 3.153$. Each interaction parameter measures the difference in slope between a given

TABLE 1. Factorial analysis of variance with logarithm of length as the dependent variable.

Source	df	SS	F-value	$P > F$
Abundance	2	4.32	187	0.0001
Age	3	44.77	1289	0.0001
Season	2	2.13	92	0.0001
Area	1	2.72	235	0.0001
Error	897	10.29		

Parameter	Estimate	SE of estimate
Intercept	5.565	0.012
Abundance		
High	−0.121	0.010
Low	0.049	0.009
Medium	0[a]	—
Age		
0	−0.741	0.017
1	−0.398	0.011
2	−0.183	0.009
3	0[a]	—
Season		
Fall	0.077	0.008
Spring	−0.065	0.012
Summer	0[a]	—
Area		
North	0.137	0.009
South	0[a]	—

[a]0 by definition.

TABLE 2. Factorial analysis of variance with logarithm of weight as the dependent variable.

Source	df	SS	F-value	$P > F$
Abundance	2	42.0	185	0.0001
Age	3	269.6	791	0.0001
Season	2	24.3	107	0.0001
Area	1	36.9	324	0.0001
Error	889	101.0		

Parameter	Estimate	SE of estimate
Intercept	5.760	0.0368
Abundance		
High	−0.365	0.0302
Low	0.184	0.0267
Medium	0[a]	—
Age		
0	−2.288	0.0527
1	−1.218	0.0337
2	−0.560	0.0295
3	0[a]	—
Season		
Fall	0.265	0.0257
Spring	−0.223	0.0377
Summer	0[a]	—
Area		
North	0.504	0.0377
South	0[a]	—

[a]0 by definition.

TABLE 3. Factorial analysis of variance with logarithm of weight as the dependent variable (logarithm of length is a covariate).

Source	df	SS	F-value	$P > F$
Abundance	2	0.0591	8.24	0.0003
Age	3	0.0645	5.99	0.0006
Season	2	0.0009	0.12	0.8859
Area	1	0.0059	1.65	0.1994
log (length)	1	55.5774	15490.18	0.0001
log (length) × abundance	2	0.0654	9.11	0.0001
log (length) × age	3	0.0640	6.08	0.0005
log (length) × season	2	0.0022	0.30	0.7391
log (length) × area	1	0.0108	3.02	0.0824
Error	880	3.1574		

Parameter	Estimate	SE of estimate
Intercept	−10.274	0.254
Abundance		
High	−0.400	0.114
Low	−0.339	0.104
Medium	0[a]	—
Age		
0	−1.406	0.353
1	−0.959	0.267
2	−0.769	0.245
3	0[a]	—
Season		
Fall	−0.055	0.113
Spring	−0.030	0.151
Summer	0[a]	—
Area		
North	−0.239	0.186
South	0[a]	—
log (length)	2.881	0.045
log (length) × abundance		
High	0.076	0.021
Low	0.068	0.019
Medium	0[a]	—
log (length) × age		
0	0.265	0.068
1	0.174	0.048
2	0.137	0.044
3	0[a]	—
log (length) × season		
Fall	0.015	0.021
Spring	0.001	0.028
Summer	0[a]	—
log (length) × area		
North	0.058	0.033
South	0[a]	—

[a]0 by definition.

level of a factor and the last level of the factor. Therefore, the interaction parameter for the last level of any factor is 0.

We see from the F-tests that the scale and the power parameters for the weight–length relationship are significantly affected by both age and abundance but not by season or area. From the estimates, we see that the scale parameter increases with increasing age and decreases slightly with increasing abundance. Even though abundance has a significant effect on the power parameter, the magnitude of the effect is relatively small biologically. Menhaden appear to have close to isometric growth, but the trend suggested by the data is that with increasing age allometric growth ($b < 3$) begins.

TABLE 4. Factorial analysis of variance. For each month, the dependent variable is the difference between log (length) for that month and log (length) for the previous month.

Source	df	SS	F-value	$P > F$
Abundance	2	0.0068	0.80	0.4496
Age	3	0.0234	1.83	0.1379
Season	2	0.0037	0.44	0.6444
Area	1	0.0086	2.02	0.1558
Error	677	2.9417		

Parameter	Estimate	SE of estimate
Intercept	0.0113	0.0083
Abundance		
High	0.0052	0.0065
Low	0.0078	0.0062
Medium	0[a]	—
Age		
0	−0.0042	0.0161
1	0.0161	0.0078
2	0.0058	0.0067
3	0[a]	—
Season		
Fall	0.0028	0.0052
Spring	−0.0079	0.0121
Summer	0[a]	—
Area		
North	−0.0086	0.0060
South	0[a]	—

[a]0 by definition.

Finally, we addressed question 4 by examining the relationship between monthly growth rates and the factors abundance, age, season, and area. The monthly growth rate for the tth month was estimated by $\log_e(L_{t+1}) - \log_e(L_t)$. Table 4 lists the results of a factorial analysis of variance with $[\log_e(L_{t+1}) - \log_e(L_t)]$ as the dependent variable and abundance, age, season, and area as factors. It is evident that none of the factors are significant.

Since growth rates do not depend upon abundance, the apparent dependence of size upon abundance noted earlier must occur primarily at times prior to recruitment. Stated differently, when compared with menhaden in years of low abundance, menhaden in years of high abundance are smaller, but this difference is due to a size differential at time of recruitment, not differences in growth rates after recruitment.

Estimation of Natural Mortality

We obtained estimates of age-specific natural mortality rates for menhaden 0, 1, 2, and 3+ yr of age by applying cohort analysis to mark–recapture data collected after 1965. The cohort analysis was based on the following equation:

$$(1)\quad Np = \sum_{t=1}^{\infty} C_t \exp\left(m(t - \tfrac{1}{2})\right)$$

where N = number of individuals marked, $1 - p$ = fraction of fish that shed tags or die from handling and tagging, C_t = catch

of marked fish in the tth month after marking, adjusted for plant-specific tag recovery efficiencies, and m = monthly natural mortality rate.

Equation 1 could easily be generalized to allow for season-specific and age-specific natural mortality. In fact, equation 1 was modified initially to allow for season-specific natural mortality estimation by age. However, season-specific estimates proved to be unstable. Therefore, age-specific natural mortalities are assumed to be season and time independent.

Estimates of handling mortality, shedding of tags, and plant tag recovery efficiencies were obtained from NMFS research. Adult menhaden handling mortality and shedding of tags were estimated to be 20% based on a tagging experiment conducted by Kroger and Dryfoos (1972, their table 3). Juvenile menhaden handling mortality and shedding of adult tags were estimated to be 35% based on a recent experiment of J. Byars (unpubl. ms, his table 1). Plant-specific efficiencies for recovering tags were obtained from a NMFS data base.

We divided the mark–recapture data into four categories. Each category is characterized by a majority of marked fish being of a given age, except that in the category of age 3+ at least 90% of the fish are age 3 or more. If it had been possible, we would have also defined the other age categories by requiring at least 90% of the fish to be of the given age. However, this would have excluded too much of the data for 1- and 2-yr-olds. The results of this majority age division are as follows:

Majority age	Age (mo)	No. of marking groups	Average marks with majority age (%)
Late juveniles	9–23	43	100
Aged 1 yr	12–23	21	69
Aged 2 yr	24–35	29	63
Aged 3+ yr	36+	7	97

Age-specific estimates were obtained in the following manner. First, we fitted equation 1 to the age 3+ category using nonlinear least-squares regression. Then we estimated the age 2 natural mortality rate by fitting the age 2 category data to equation 1, modified to allow for age-specific natural mortality and with the age 3+ natural mortality parameter fixed at the value obtained from the first regression. Continuing in this manner, we obtained estimates of natural mortality for age 1 and 0 menhaden.

In each of the above regression analyses, both unweighted and weighted nonlinear least-squares was tried. The weighted method, which minimizes (observed − expected)^2/expected, provided slightly less variable estimates in all cases. Results of the weighted regressions appear in Table 5.

Natural mortality appears to be almost constant for released fish that are late juvenile and ages 2 and 3+. The estimated natural mortality for age 1 is very low. The coefficient of variation there is very high, but this is due to the low estimate, not a large standard deviation. The juvenile and age 1 categories should have approximately the same natural mortality rates, since their ages overlap substantially. Because the age-specific natural mortalities for ages greater than the one being estimated are assumed to be known without error, there is a propagation of error corresponding to each step except the first in the estimation process. Therefore, the estimates for age 0 and 1 fish are less reliable than those for age 2 and 3+ fish. It is this propagation of error that may have caused the low age 1 natural mortality estimate. Other factors such as an unusually low shedding loss of tags, low tagging and handling mortality, and the breakdown of the season- and time-independent assumptions could also be responsible for this low age 1 estimate.

TABLE 5. Natural mortality estimates by age of menhaden obtained from weighted regression of equation 1 (C.V. = coefficient of variation).

Category	Age (mo)	Monthly M (annual)	SD	% C.V.
Late juvenile	9–23	0.045 (0.540)	0.012	27
Age 1	12–23	0.013 (0.151)	0.014	110
Age 2	24–35	0.041 (0.486)	0.014	35
Age 3+	36+	0.043 (0.518)	0.006	13

Our estimates of natural mortality are comparable (except for the age 1 category) with the annual $m = 0.52$ value obtained by Dryfoos et al. (1973) from mark–recapture data.

Estimation of Migration

We estimated migration by analyzing catch (in numbers of fish by age, month, and area) and effort data (in numbers of days landed by month and area; Henry 1971). This analysis was based on the following reduced equation:

$$(2)\quad \mathrm{CPUE}_t(j) = \sum_{i=1}^{4} \theta(i, j)\mathrm{CPUE}_{t-1}(i) \times \exp\{-m - 0.5q[E_t(j) + E_{t-1}(i)]\}$$

where $\mathrm{CPUE}_t(j)$ = catch per unit effort during month t in area j, $\theta(i, j)$ = probability of migration from area i to area j at the end of the month t, q = catchability coefficient, $E_t(j)$ = fishing effort for month t and area j, and m = natural mortality rate determined in the previous analysis (the estimate for late juveniles was also used for age 1 menhaden). For further details concerning the derivation of equation 2 and its application to Atlantic menhaden see Deriso et al. (1983).

We fitted equation 2 to each combination of age and season. Seasons are the same as those defined for the growth analyses. We also applied the logarithm transformation to equation 2 in order to obtain stable estimates and homoscedastic and normally distributed errors. Such a transformation has been used successfully for catch-effort data on the other fish stocks (Palaheimo 1961; Pope 1977). Except for the fall season data, the log-transformed data yielded residual plots showing no violations of the homoscedastic and additive normal error assumptions.

We fitted equation 2 to the fall season data by applying robust regression (Huber 1973, 1977; Andrews 1974). Compared with least-squares estimation, robust estimation is much less sensitive to nonnormal errors, heteroscedasticity, and the presence of outliers. The particular robust method that we employed is discussed in Deriso et al. (1983).

All fits of equation 2 for the spring and summer season are highly significant, except for the spring season for age 3+, which is based on only 16 degrees of freedom. Average migration can best be characterized by examining the estimated average migration probabilities for age 2 menhaden (Table 6).

Figure 1 is a graphical presentation of the fit of our regression model. In this graph, we plotted observed and predicted values of CPUE separately by age against time (on a seasonal resolution) from 1965 to 1978. The predicted values follow the observed values reasonably well, except that very large observed

TABLE 6. Estimated average migration probabilities and their standard errors for age 2 Atlantic menhaden.

Season[a]	θ (1,1)[b]	θ (1,2)	θ (2,1)	θ (2,2)	θ (2,3)	θ (3,2)	θ (3,3)	θ (3,4)	θ (4,3)	θ (4,4)
1	1.00[c] (—)	0.00[c] (—)	0.39 (0.295)	0.61 (0.295)	0.00[c] (—)	0.52 (0.264)	0.48 (0.264)	0.00[c] (—)	0.40 (0.082)	0.60 (0.082)
2	0.83 (0.136)	0.17 (0.136)	0.05 (0.016)	0.61 (0.107)	0.34 (0.108)	0.21 (0.052)	0.62 (0.094)	0.17 (0.125)	0.22 (0.095)	0.78 (0.095)
3	0.002 (0.672)	0.998 (0.672)	0.00[c] (—)	0.60 (0.125)	0.40 (0.125)	0.00[c] (—)	0.72 (0.055)	0.28 (0.055)	0.00[c] (—)	1.00[c] (—)

[a]Seasons: 1 = February–May; 2 = May–August; 3 = August–February.
[b]Areas: 1 = North Atlantic; 2 = mid-Atlantic; 3 = Chesapeake Bay; 4 = South Atlantic.
[c]Assumed value.

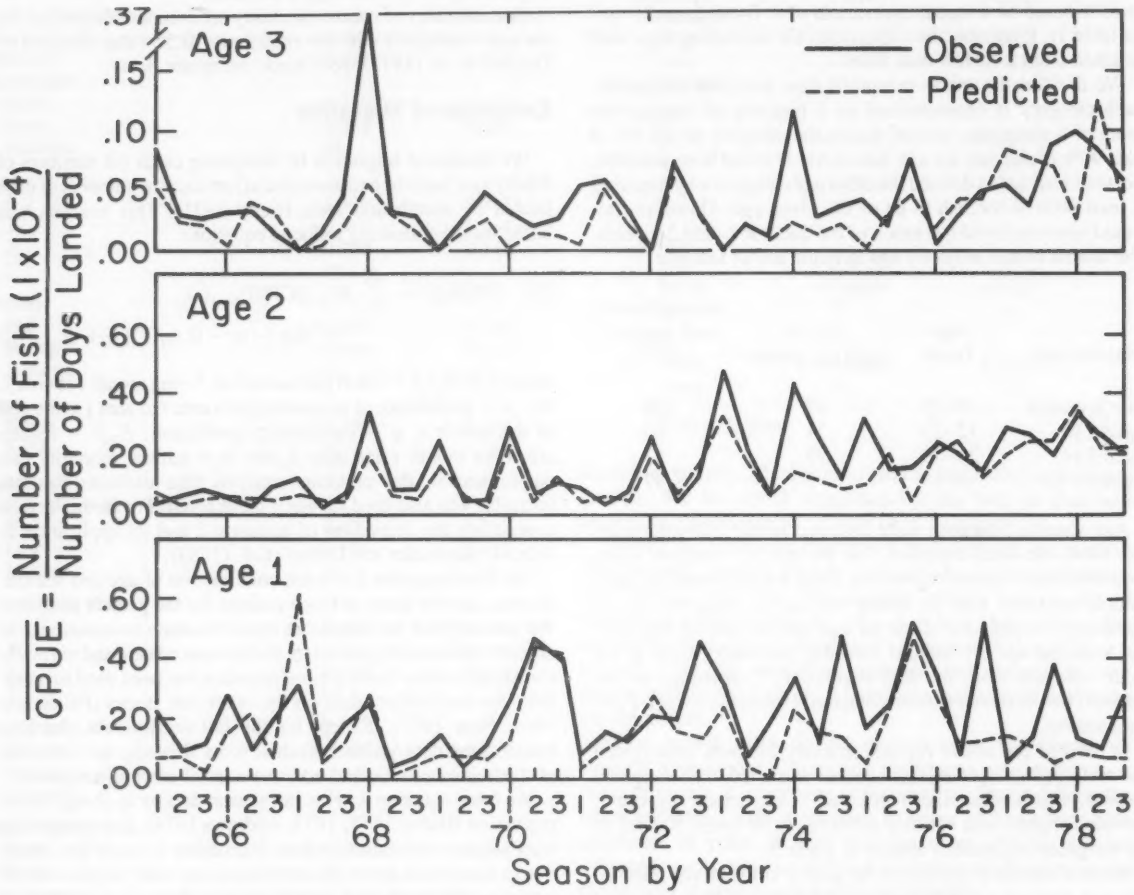

FIG. 1. Comparison of observed CPUE and CPUE as predicted by regression using equation 2.

CPUE values are not predicted well. This underprediction is partially related to the use of the log transform or robust methods in the regression analysis. If least-squares regression is applied without the log transformation or robust methods, then the selected model would better predict large CPUE values, but it would not predict the majority of the CPUE values well. The basic cause of prediction error, of course, is that no model can completely incorporate all biological complexities, even if these were understood. By choosing to use the log transform and robust methods, we decided to predict typical CPUE values well, at the expense of underpredicting very large values. In general, the estimated migration probabilities seem biologically plausible, i.e. seasonal changes in the age-specific migration probabilities reflect major shifts in area-specific CPUE. However, age 2 menhaden data seem most reliable and those migration probabilities probably best characterize average menhaden movements (Table 6).

Our regression results indicate that migration probabilities

are age specific, especially in the summer season. Age 1 fish are less likely to move from area 3 to area 2 than age 2 or 3+ menhaden. Age 3+ fish are more likely to move from area 2 to area 1 than age 2 menhaden. Some bias may be present in estimated migration probabilities due to two sources: (1) vessels may catch fish in one area and unload these fish in another area and (2) some first-time recruitment of age 1+ fish into the "fishable" population may occur during the three seasons. Our methodology is such that it allows an impulse of new recruits at the beginning of each season, so the second source of bias is mitigated to some extent.

Estimation of Fishing Mortality

We estimated age- and season-specific catchability coefficients along with migration probabilities from the nonlinear regression of equation 2. The only estimates for catchability coefficients, which were not forced to their lower constraint, 0.0001, by the nonlinear algorithm, were those in the summer season for all ages and one in the fall season for age 2. However, the only catchability coefficients that differ significantly from zero were those for age 2 menhaden. These catchability coeffiients of 0.08 and 0.15 coupled with their corresponding averaged efforts[2] (2.27 and 0.62) produced average monthly fishing mortality rates of 0.18 and 0.09 for age 2 fish during the summer and fall seasons, respectively. However, when allowing for the variability in the catchability coefficient estimates, these calculated fishing mortality rates were found not to be statistically different.

We implemented cohort analysis on yearly catch data from 1955 to 1978 to estimate yearly age-specific population levels ($N_{a,t}$) (Deriso et al. 1983). The following relationship was used to calculate yearly fishing mortality rates ($F_{a,t}$) by age (a), independent of fishing effort data:

$$(3)\quad F_{a,t} = \log_e (N_{a,t}) - \log_e (N_{a,t+1}) - M_a$$

where M_a is the natural mortality estimate for age a as determined from mark–recapture data (the estimate for late juveniles was also used for age 1 menhaden).

To compare nonrecruited age 0 fish with recruited older aged fish, we computed monthly recruited fishing mortality rates from the yearly rates produced from equation 3. These monthly fishing mortality rates for age 0, 1, 2, and 3 menhaden are plotted by year in Fig. 2. Unlike the age 2 and 3 fishing mortality rates, the instantaneous fishing mortalities for age 1 remain fairly constant from one year to the next whereas the fishing mortality rates for age 2 and 3, which follow a similar time series, demonstrate more erratic behavior and an increasing trend from early in the 1960's to the present.

Spawner–Recruit Analysis

The numbers of recruits in the spawner–recruit analysis for the years 1955–75 were calculated using cohort analysis (Deriso et al. 1983). Because we measured the size of the spawning stock in February and the recruitment in the following fall, the recruits in a given year-class are the offspring of the spawners of the same year. Age-specific percent mature females, egg contributions, and a female age–length equation, taken from Higham and Nicholson (1964) and Reintjes (1969), and age-specific abundances calculated from cohort analysis were used to calculate the numbers of eggs in each of the 21 yr. A scatter plot of these data (Fig. 3) fails to reveal any obvious relationship between eggs and recruits. The data range from a low of 15×10^{12} eggs in 1969 to a high of 262×10^{12} eggs in 1961.

Environmental variables considered in our analysis consist of temperature and Ekman transport. North, mid-, and South Atlantic average temperatures during the peak spawning period each year were approximated using meteorological data from coastal cities (Deriso et al. 1983), and North, mid-, and South Atlantic westward Ekman transports for each year were taken from Nelson et al. (1977). In all cases, eggs are in units of 10^{12}, recruits are in units of 10^9, temperature is in degrees Celsius, and Ekman transport is in units of 10^2 metric tons × kilometres per second.

We considered the environmental variables to have a multiplicative effect on the number of eggs in determining the number of recruits (Ricker 1975). The environmental variables, $X_1, \ldots, X_6$ (North, mid-, and South Atlantic temperatures and North, mid-, and South Atlantic westward Ekman transports, respectively), were incorporated into standard spawner–recruit models by using the effective number of eggs (S) in place of the number of eggs (E). Parameter S is defined as

$$(4)\quad S = E \exp\{\beta_1 X_1 + \ldots + \beta_6 X_6\}$$

where $\beta_1, \ldots, \beta_6$ are unknown coefficients to be estimated in the analysis.

The Beverton–Holt model used was

$$(5)\quad R = \{\alpha_{BH} + \beta_{BH}/S\}^{-1}$$

where R is the number of recruits, $\alpha_{BH} \geq 0$ and $\beta_{BH} \geq 0$ are unknown parameters that are to be estimated, and S is the effective number of eggs, as defined above.

We fitted the full model, i.e. equation 4 substituted in equation 5, with three different sets of constraints on the parameters. In all cases, we constrained α_{BH} and β_{BH} to be nonnegative. For the first fit this was the only constraint. For the second fit, we constrained $\beta_1, \ldots, \beta_5$ to be zero, so that the South Atlantic westward Ekman transport was the only environmental factor in the model. (This was done because Nelson et al. (1977) found westward Ekman transport in the South Atlantic of value in modeling the menhaden egg–recruit relationship.) In the third fit, we constrained $\beta_1, \ldots, \beta_6$ to be zero, so that no environmental factors entered into the model.

The unnormalized gamma model used was

$$(6)\quad R = \alpha_R S^{\gamma} \exp\{-\beta_R S\}$$

where R is again the number of recruits, $\alpha_R \geq 0$, $\beta_R \geq 0$, and γ are unknown parameters that are to be estimated, and S is the effective number of eggs, as defined above. We fitted this full model, i.e. equation 4 substituted in equation 6, to the data with α_R and β_R constrained to be nonnegative, and with the same three sets of constraints on $\beta_1, \ldots, \beta_6$ as defined above with the Beverton–Holt model.

We investigated the unnormalized gamma function because it includes as a special case the Ricker curve ($\beta_1 = \ldots = \beta_6 = 0$ and $\gamma = 1$) and can be made to closely approximate the Beverton–Holt curve ($\beta_1 = \ldots = \beta_6 = 0$, $\beta_R = 0$, and $\gamma < 1$). Therefore, it may be thought of as a compromise between the two.

We also examined the inverted forms of the full models with $\beta_1 = \ldots = \beta_6 = 0$ because the inverse transformed data display

[2]Effort in units of vessel-days-landed scaled by a factor of 1/60 (Henry 1971).

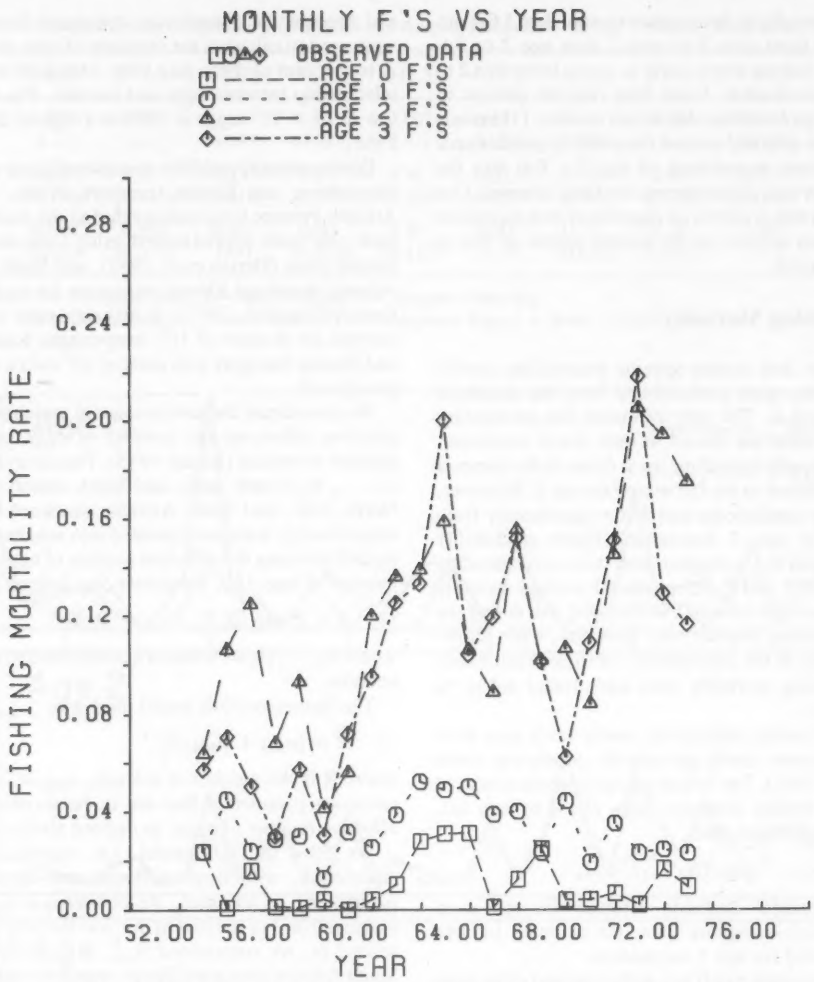

FIG. 2. Monthly age-specific fishing mortality rates plotted against year of occurrence.

no violations of the homoscedastic and normal error assumptions. For the inverted Beverton–Holt, $R^2 = 0.217$, and for the inverted unnormalized gamma model, $R^2 = 0.224$. These are the only models fit in the spawner–recruit analysis that are significantly different from constant recruitment. The Beverton–Holt model is significant at the 0.017 level, and the unnormalized gamma model is significant at the 0.100 level. The test for the Beverton–Holt model is one-sided, since it is known that $\beta_{BH} \not< 0$. The test for the unnormalized gamma model is the usual two-sided test, so even though the Beverton–Holt model is more significant, it is not as much as these figures may seem to imply.

Use of the inverse transform causes smaller predicted numbers of recruits. For typical recruitment, these smaller predictions are closer to observed values, but for the years with large recruitment, the inverted models underpredict by a greater margin than their untransformed counterparts.

The parameter estimates from the fits of the untransformed Beverton–Holt and unnormalized gamma models are presented in Table 7. Note that the estimated deviations are large in comparison with the parameter estimates. The observed recruits, the predicted recruits from the fits with only westward Ekman transport from the South Atlantic as an environmental factor, and the two predictive curves from the fits with no environmental factors are displayed in Fig. 3. From this plot it is evident that the unnormalized gamma model is more responsive to the inclusion of the environmental parameters than is the Beverton–Holt model.

Neither of the full models (all environmental factors included) with the estimates derived from these data are appropriate for simulation purposes, as estimating 8 or 9 parameters from 21 data points has caused extremely high variances. For descriptive purposes, the unnormalized gamma curve with westward Ekman transport for the South Atlantic offers a reasonable compromise between too many parameters and too poor a description of the data.

Examination of the recruitment data revealed that in 1958 the Ekman transport for the South Atlantic had its largest value and the number of recruits was twice as large as in any other year, but the number of eggs in 1958 was less than the number of eggs in 7 of the other 20 yr. This has led to speculation that the 1958 data point is responsible for the benefits of including the South

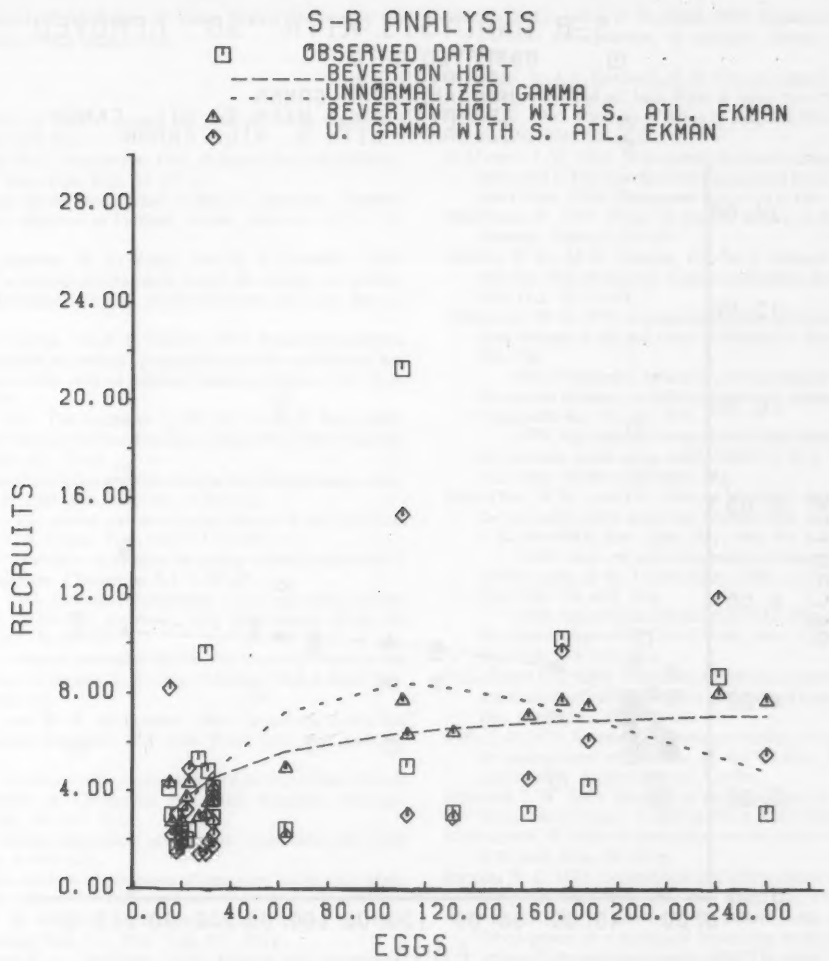

FIG. 3. Recruits (units are 10^9 fish) vs. eggs (units are 10^{12} eggs): recruits observed, predicted by Beverton–Holt and unnormalized gamma models with South Atlantic Ekman transports, and curves estimated by Beverton–Holt and unnormalized gamma models with no environmental factors.

TABLE 7. Results of the spawner–recruit analysis. Untransformed models (5 and 6) with all data included. Eggs were in units of 10^{12}, recruits were in units of 10^9, β_1 to β_3 are coefficients of temperatures (°C), and β_4 to β_6 are coefficients of Ekman transports in units of $10^2 \times$ km/s.

Model	R^2	Estimates (SD)								
		α	β	γ	β_1	β_2	β_3	β_4	β_5	β_6
Beverton–Holt with no environmental factors	0.129	0.128 (0.040)	3.14 (2.48)							
Beverton–Holt with South Atlantic Ekman transport	0.186	0.115 (0.034)	5.79 (4.59)							0.013 (0.048)
Beverton–Holt with all environmental factors	0.240	0.097 (0.037)	11.3 (58.1)		0.065 (1.18)	−0.095 (1.68)	0.057 (0.91)	−0.0002 (0.058)	−0.0056 (0.064)	0.023 (0.176)
Unnormalized gamma with no environmental factors	0.184	0.130 (0.286)	0.010 (0.008)	1.12 (0.674)						
Unnormalized gamma with South Atlantic Ekman transport	0.524	0.593 (0.533)	1.32×10^{-23} (7.34×10^{-6})	0.293 (0.151)						0.068 (0.034)
Unnormalized gamma with all environmental factors	0.740	0.046 (0.172)	8.27×10^{-25} (2.27×10^{-16})	0.168 (0.152)	0.57 (1.11)	−0.27 (1.67)	1.07 (1.60)	0.059 (0.085)	−0.053 (0.074)	0.104 (0.127)

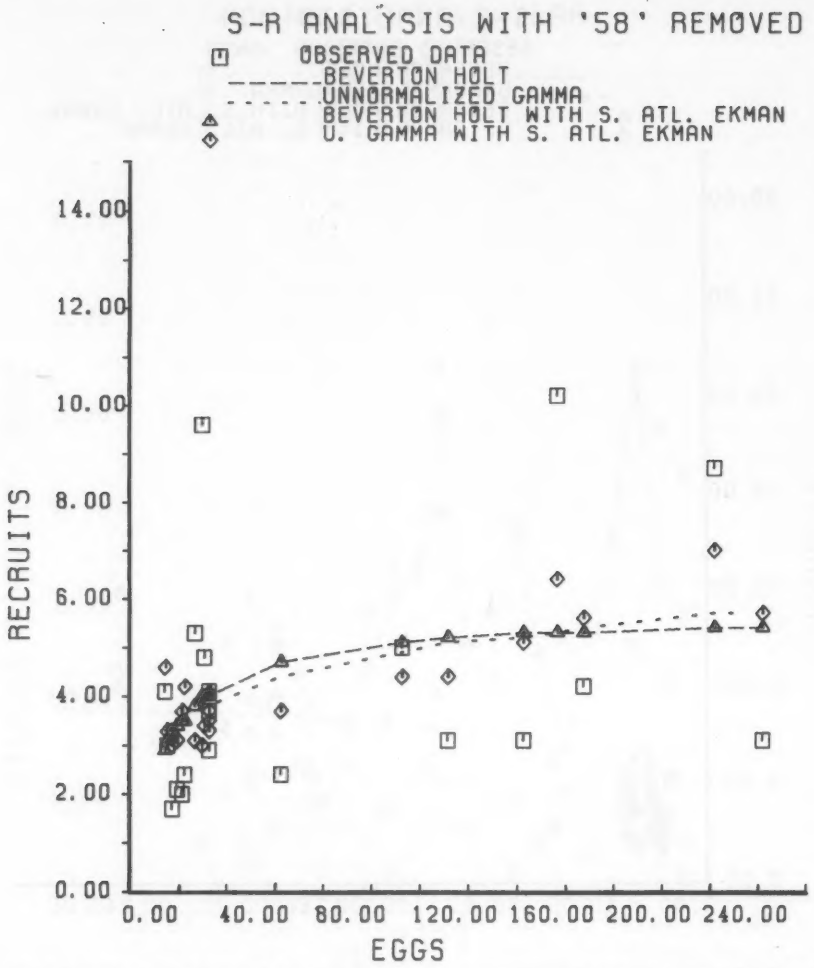

FIG. 4. Recruits (units are 10^9 fish) vs. eggs (units are 10^{12} eggs): recruits observed, predicted by Beverton–Holt and unnormalized gamma models with South Atlantic Ekman transports, and curves estimated by Beverton–Holt and unnormalized gamma models with no environmental factors. The 1958 observation was deleted from the analysis.

Atlantic westward Ekman transport in the models. To investigate this suggestion, we repeated the analysis with the 1958 data point deleted from the data set (Fig. 4). The improvement due to including the westward Ekman transport for the South Atlantic is not as good as before. There is little justification for including any of the environmental parameters. Note that this fitted unnormalized gamma curve without environmental parameters will attain its maximum at around 2020×10^{12} eggs, more than 7 times the largest observed value. It is the 1958 observation that caused the unnormalized gamma curve to decrease within the range of the data (Fig. 3). Therefore, there is little evidence in these data to support overcompensation at high egg production levels.

The egg–recruit relationship is so variable that any nonstochastic spawner–recruit model is highly unrealistic at this time. The inverted Beverton–Holt model offers a reasonable structure for describing such a stochastic egg–recruit relationship. In the inverted forms of the models, the stochastic error components were shown to follow an independent normal distribution with a mean of zero and a constant variance. Since there is little evidence supporting overcompensation, since the Beverton–Holt model is the only model significantly different from constant recruitment at the 0.05 probability level, and since the Beverton–Holt model has one less parameter than the unnormalized gamma function, it is preferred for simulation purposes. If important environmental determinants of recruitment are eventually recognized, then deterministic spawner–recruit models using environmental variables may become satisfactory for modeling. However, environmental variables are random, so a stochastic model would still be needed for forecasting.

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Environmental Effects on Recruitment, Growth, and Vulnerability of Atlantic Herring (*Clupea harengus harengus*) in the Gulf of Maine Region[1]

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Anthony, V. C., and M. J. Fogarty. 1985. Environmental effects on recruitment, growth, and vulnerability of Atlantic herring (*Clupea harengus harengus*) in the Gulf of Maine region. Can. J. Fish. Aquat. Sci. 42(Suppl. 1): 158–173.

Atlantic herring (*Clupea harengus harengus*) recruitment in the Gulf of Maine since 1947 has varied by a ratio of 20 to 1. Since heavy fishing began in the mid-1960's, recruitment has fluctuated by only a factor of 9 to 1. The greatest fluctuations in recruitment, therefore, historically occurred in the absence of high fishing mortality. Recruitment predictions and understanding of the causes of fluctuations are extremely important, since strong year classes traditionally have sustained the herring fisheries in the Gulf of Maine. The effect of environmental variables (particularly temperature) on herring recruitment and growth were examined in detail. Vulnerability of Gulf of Maine herring in response to moon phase is also considered. Indices of abundance of Atlantic herring in the Gulf of Maine were calculated for three time periods using three different procedures. Indices of abundance for the periods of 1915–67 and 1951–81 indicated that productivity, or amount of recruitment per amount of spawning stock, was positively related to temperature or other factors (e.g. food availability) related to temperature at intermediate to high levels of spawning stock biomass. For the shorter and most recent time period (1965–81), abundance was calculated by virtual population analysis and an attempt was made to relate temperature effects during several periods in the first year of life to recruitment levels at age 2. The mean, maximum, and minimum water temperatures during (1) September–December (spawning – early larval development), (2) January–April (overwintering and late larval development), and (3) May–August (postlarval) periods were correlated with abundance. Significant effects of mean and minimum temperature during period 2 and minimum temperature during period 3 were observed, suggesting that environmental influences on determination of year class strength occur during late larval – early juvenile phases. Possible reasons for the discrepancy between the long-term analyses bases on abundance indices and the more detailed analyses using population size estimates based on virtual population analysis are discussed. An indication of environmental limitation is also shown by density-dependent growth. Growth appears to be related to both age 2 abundance and summer water temperature. When abundance is great, its effect overcomes the positive effect of temperature (or other factors indicated by temperature). The environment also alters the availability and vulnerability of herring to the inshore fisheries. Young herring are more available and vulnerable to fixed gear during the dark phase of the moon. This effect is pronounced when abundance is low.

Depuis 1947, le recrutement du hareng de l'Atlantique (*Clupea harengus harengus*) dans le golfe du Maine a varié suivant un rapport de 20 pour 1. Depuis que la pêche intensive a commencé vers le milieu des années soixante, le recrutement n'a fluctué que par un facteur de 9 pour 1. Les fluctuations les plus importantes se sont donc produites alors que la pêche n'était pas encore un facteur de mortalité élevée. Il est très important de prévoir le recrutement et de connaître les causes des fluctuations, car de longue date la pêche au hareng dans le golfe du Maine dépend des classes d'âge fortes. On a étudié de façon approfondie les effets des facteurs du milieu (en particulier de la température) sur le recrutement et la croissance du hareng. On s'est également penché sur la vulnérabilité de ce poisson en fonction du cycle lunaire. Au moyen de trois méthodes différentes, on a déterminé la valeur de divers indices représentant l'abondance du hareng de l'Atlantique dans le golfe du Maine durant trois périodes distinctes. Les résultats montrent que de 1915 à 1967 et de 1951 à 1981, il y a une relation positive entre la productivité, ou recrutement en fonction de l'importance du stock de frai, et la température ou d'autres facteurs liés à la température (par ex., l'abondance de la nourriture) lorsque la biomasse du stock de frai est modérément ou fortement élevée. Dans le cas de la période plus récente et plus courte (de 1965 à 1981), on a déterminé l'abondance des poissons par une analyse de la population virtuelle et on a essayé de voir s'il y avait un lien entre les effets de la température durant diverses phases de la première année d'existence et le recrutement à deux ans. On a étudié la relation entre l'abondance et la température moyenne, la température maximum et la température minimum durant les trois périodes suivantes : (1) de septembre à décembre (frai et premiers stades du développement larvaire); (2) de janvier à avril (hivernage et derniers stades du développement larvaire); et (3) de mai à août (phase post-larvaire). On a constaté que le température moyenne et la

[1]This paper was presented at the International Symposium on the Biological Characteristics of Herring and Their Implication for Management, convened at Nanaimo, B.C., June 20–22, 1983, commemorating the 75th anniversary of the Pacific Biological Station.

température minimum ont des effets significatifs durant la deuxième période et que la température minimum influe en outre sur la troisième période, ce qui indiquerait que les facteurs du milieu influent sur la force d'une classe d'âge vers la fin du développement larvaire et au début du stade juvénile. On examine les raisons qui pourraient expliquer la différence entre les résultats des analyses à long terme basées sur les indices d'abondance et ceux des analyses plus détaillées basées sur l'importance des populations estimées d'après les populations virtuelles. Le fait que la croissance soit liée à la densité laisse également supposer que le milieu peut être un facteur limitant. La croissance semble dépendre de l'abondance à deux ans et de la température de l'eau durant l'été. L'abondance des poissons a des conséquences qui neutralisent les effets positifs de la température (ou des facteurs liés à la température). Les facteurs du milieu influent également sur l'abondance et la vulnérabilité du hareng dans les pêches intérieures. Le jeune hareng est plus abondant et plus facile à pêcher avec des engins fixes durant la phase de décroissance du cycle lunaire. Cet effet est prononcé lorsque les poissons sont peu nombreux.

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The Atlantic herring (*Clupea harengus harengus*) has long supported important commercial fisheries throughout coastal regions of the North Atlantic; accordingly, considerable attention has been devoted to determining factors influencing year class success. Among the most striking characteristics of clupeoid stocks, in fact, is high variability from year to year in recruitment levels. Cushing (1971) attributed this variability to the lack of strong density-dependent regulatory mechanisms. Cushing (1975) and Cushing and Dickson (1976) also proposed that survival of first-feeding larval Atlantic herring is largely dependent on synchrony between spawning periodicity and availability of potential prey. Spawning periods were shown to be relatively fixed, and it was hypothesized that annual variation in the timing of plankton blooms may result in a "match" or "mismatch" between larvae and their principal prey, thus causing wide density-independent variability. Hjort (1914) had earlier suggested that catastrophic mortality among post-yolk sac herring larvae may occur due to lack of suitable prey or passive transport to unfavorable locations.

Abiotic effects on survival and predation have also been implicated as determinants of year class strength in clupeoids (see reviews by Blaxter and Hunter 1982; Cushing and Dickson 1976). The importance of considering environmental influences on marine fish populations is reflected in a recent scientific program proposed by the Food and Agricultural Organization in 1979 (Sullivan 1982). The proposed program identified five variables that were most likely to determine recruitment levels. These were temperature, turbulence, transport, food, and predation.

Indices of herring year class strength have been variously related to water temperature (Craig 1960; Postuma and Zijilstra 1974; Lett and Kohler 1976; Sinclair et al. 1982b), wind strength and/or direction (Carruthers 1951; Craig 1960; Sinclair et al. 1982a), winter phosphorus (Cushing and Dickson 1976), salinity (Bowers and Brand 1973), sea level (Sinclair et al. 1982a), and interactions with Atlantic mackerel (*Scomber scombrus*) (Winters 1976; Lett and Kohler 1976; Skud 1982). Significant correlations between Atlantic herring landings and water temperature were reported by Dow (1977) and Sutcliffe et al. (1977).

In this paper, we examine environmental influences on Atlantic herring recruitment, growth, and vulnerability in the Gulf of Maine region with particular emphasis on temperature-related effects. Detailed abundance data are available since 1965, based on virtual population analysis (VPA, Gulland 1965a). Two general methods of estimating abundance were used for two earlier periods (1915–67 and 1951–81) to relate changes in abundance to water temperature. Stock and recruitment relationships are examined and possible temperature-related effects are considered. The effects of water temperature and density on growth are examined, as are the effects of the phase of the moon on "sardine" catches.[2]

Herring Fisheries and Biology in the Gulf of Maine – Georges Bank Area

Three major herring stocks and several minor stocks historically have existed in the Gulf of Maine region. Major herring stocks are located on Georges Bank, southwestern Nova Scotia, and Jeffreys Ledge (western Gulf of Maine) and have supported important fisheries. Small-scale but consistent spawning occurs at several other locations in the Gulf of Maine such as near Nantucket Shoals, in several areas along the Maine coast, near Grand Manan, and in the Bay of Fundy. The Maine and New Brunswick coast juvenile herring fisheries probably catch herring from several stocks. While tagging (Stobo 1983) and meristic studies (Anthony 1981; Anthony and Boyar 1968) have elucidated the stock definition in general for adult herring, many of the details of the stock structure are still not clear. For purposes of this paper we assume that the juvenile herring along the Maine coast would recruit to the adult fishery in the western Gulf of Maine area (Jeffreys Ledge stock). Catches from the Jeffreys Ledge area and from the Maine coast were thus combined to generate estimates of abundance based on VPA for comparison with environmental data. While this may not represent the final delineation of stock components and thus combination of herring catches for estimating abundance in the western Gulf of Maine area, it should provide useful estimates for the purposes of the following analyses.

The most significant herring fisheries in the Gulf of Maine region historically have been "sardine" fisheries (Maine and New Brunswick), which began in 1875 and were the main fisheries for herring in the Gulf of Maine region until the mid-1960's (Table 1). Fisheries for large herring (mostly adult herring) began on Georges Bank in 1961 and on the spawning grounds of Jeffreys Ledge in the western Gulf of Maine in 1967. A small fishery for large herring also expanded greatly in 1965 off southwestern Nova Scotia. Catches increased greatly in the late 1960's throughout the entire Northwest Atlantic (Fig. 1) but declined rapidly. The Georges Bank fishery collapsed by 1977, and the adult fishery off Nova Scotia is gradually declining

[2]Juvenile herring, when sold in cans, have been called sardines.

TABLE 1. Herring catches (t) in major fishing areas of the Northwest Atlantic for the years 1950–79.

Year	Maine juvenile fishery	Gulf of Maine adult fishery	Georges Bank	New Brunswick juvenile fishery	Nova Scotia adult fishery	Gulf of St. Lawrence and Newfoundland fishery	Total
1950	90 557	3 661		62 981[a]		60 707	217 906
1951	34 411	1 305		51 316[a]		64 671	151 703
1952	79 139	1 598		62 399[a]		64 555	207 691
1953	58 337	2 032		44 961[a]		49 632	154 962
1954	64 067	1 303		46 716[a]		54 706	166 792
1955	43 506	1 561		33 313[a]		52 804	131 184
1956	66 494	2 058		21 533	22 712	41 547	154 344
1957	68 625	3 007		33 733	27 114	36 479	168 956
1958	80 759	3 182		18 854	46 444	38 156	187 385
1959	53 057	1 472		47 762	28 771	28 943	159 985
1960	59 348	1 126		49 563	32 216	27 401	169 654
1961	24 131	3 178	67 655	18 614	41 272	23 188	178 038
1962	69 376	2 485	152 242	34 403	35 367	48 568	342 441
1963	66 895	3 217	97 968	41 450	27 233	46 354	283 117
1964	26 295	8 815	131 438	49 748	44 851	46 899	308 046
1965	32 088	2 635	42 882	49 101	82 074	56 340	265 120
1966	26 177	4 360	142 704	61 395	130 501	65 316	430 451
1967	28 576	7 807	218 743	50 920	140 689	145 966	592 701
1968	31 072	31 900	373 598	79 094	151 238	278 651	945 553
1969	23 852	32 406	310 758	44 832	137 267	383 903	933 018
1970	15 617	40 187	247 294	33 134	178 422	337 920	852 574
1971	12 408	38 575	267 347	17 513	128 450	279 038	743 331
1972	19 498	42 918	174 190	33 046	144 230	130 206	544 088
1973	16 400	15 926	202 333	27 814	112 515	103 929	478 919
1974	19 142	18 098	149 525	29 159	143 590	62 194	421 708
1975	15 182	21 530	146 096	25 020	158 125	63 294	429 247
1976	30 195	20 125	43 502	33 234	102 670	66 072	295 798
1977	32 357	17 891	2 157	24 724	105 744	70 891	253 764
1978	29 858	18 558	2 059	39 882	101 925	78 130	270 412
1979	40 218	23 546	1 270	41 021	47 488	71 470	225 013
1980	45 902	36 175	1 319	14 968	107 301	68 537	274 583
1981	48 245	15 321	672	20 447	83 814	40 194	208 693
1982	24 007	7 663	1 378	26 066[b]	78 705[b]	35 194[b]	173 013[b]
Total	1 375 769	435 621	2 777 503	1 268 714	2 440 728	3 021 355	11 319 690

[a]Cannot be separated into juvenile and adult.
[b]Preliminary figures.

under intense fishing pressure. The western Gulf of Maine adult fishery (Jeffreys Ledge stock) has recently declined due to market constraints. Descriptions of the population dynamics of Gulf of Maine herring fisheries are found in Anthony (1972), and the Georges Bank herring fishery has been reviewed by Anthony and Waring (1980a).

Catches by age from the Maine coastal fishery are presented in Table 2. Age determination protocol developed in the early 1960's assigns a January 1 birthdate; thus, a fish spawned in autumn will be categorized as age 0 until January when they then become age 1 at an actual age of 3–4 mo. Detailed catch statistics for this fishery are available from 1947 to the present but biological sampling for age and growth has only been available since 1962. A breakdown of ages prior to 1962 was accomplished by converting the number of cases of "sardines" packed according to the number of fish per can to length and then to age by week and by small areas along the Maine coast (Anthony 1972). Age 1 and 2 herring do not overlap in length during the summer fishing season, and catches of age 1 herring according to the number packed per sardine can are in fact very reliable. The method is not very useful for separating age 3 and age 4 herring. In earlier years, however, very few large herring were harvested.

Within the Gulf of Maine – Georges Bank area, spawning occurs during August–November, with peak spawning during September–October (see review by Anthony and Waring 1980b). Maturation begins at age 3 and Gulf of Maine herring are fully recruited to the spawning stock by age 5. Larvae spawned in immediate coastal areas are thought to overwinter within estuarine nursery areas (Graham et al. 1972). Herring larvae from spawning areas offshore, such as on Georges Bank, however, may overwinter in offshore areas. The extended larval phase is terminated in late spring following metamorphosis into a juvenile stage ("brit"), which forms large feeding aggregations during summer. By the end of the first year of life, the juveniles are partially recruited to the coastal fisheries at about 12 cm in total length.

The recent recruitment levels (age 3 abundance as calculated from virtual population analyses) of the Gulf of Maine, Nova Scotia, and Georges Bank adult herring fisheries are compared

FIG. 1. Catches of Atlantic herring from the Northwest Atlantic.

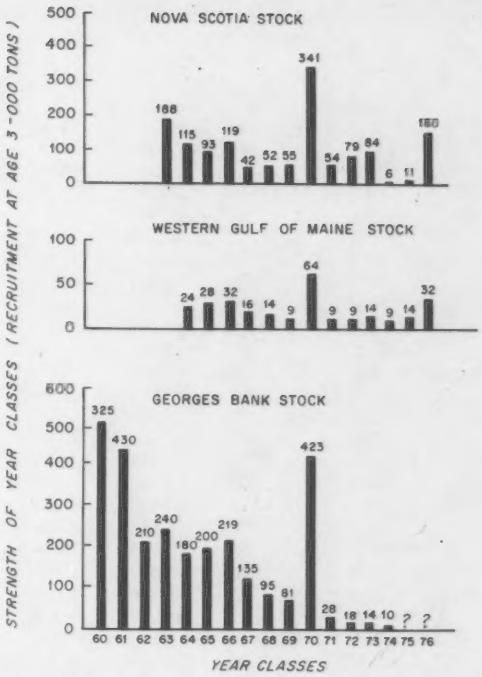

FIG. 2. Comparison of recent recruitment levels to Gulf of Maine adult herring stocks.

in Fig. 2. In general there is a clear correspondence of strong and weak year classes for these stocks. The strong 1963, 1966, 1970, and 1976 year classes and the weak 1967–69 and 1971–72 year classes are common in each of the three herring fisheries. The 1960 and 1961 year classes, in addition, are known to have been excellent in the Nova Scotia fishery and in the Maine juvenile fishery although estimates of absolute abundance were not available. Intense fisheries have existed on age 1 and 2 herring along the Maine and New Brunswick coasts but not on Georges Bank, Jeffreys Ledge, or on the Nova Scotian Shelf. Comparisons of year class abundance, therefore, could only be made at age 3 or older. In all juvenile fisheries, however, the catches at age 1 and age 2 reflect clearly the same strong and weak year classes as noted above. Since the estimates of absolute stock abundance, fishing mortality, and the type of fishing varied among the Gulf of Maine, Nova Scotia, and Georges Bank adult fisheries and the fisheries are distinct on separate spawning grounds, the agreement in year class strengths is probably a function of a widespread environmental phenomenon. The strengths of the year classes were also obvious in the juvenile fishery; therefore, the abundance of each year class was set prior to age 2.

Effect of Temperature on Recruitment

Qualitative insight into general relationships between water temperature and Gulf of Maine herring yield may be provided by examining covariation between temperature and landings records for the coast of Maine. Surface water temperatures increased along the Maine coast during the late 1940's and remained at high levels through the middle of the 1950's (Welch 1982). Water temperatures declined fairly steadily until the late 1960's when they again increased to intermediate levels (Fig. 3). A general correspondence was noted between mean seawater temperatures at Boothbay Harbor during September–March and Maine herring catches. Temperature values have been lagged by 2 yr to represent temperature conditions during the first 6 mo of larval life. The juvenile herring fishery is selective for age 2 herring (Anthony 1972) and, therefore, a lag of 2 yr is appropriate for a high proportion of the catch.

Catches increased to near record levels during the 1950's coincident with increased water temperature (Fig. 3), suggesting a positive correlation between temperature and yield. Unfortunately, measures of absolute abundance do not exist for this early period and landings data must be used as an index of abundance. As a result, we are unable to separate the effects of abundance and availability. The magnitude of the catches does indicate high abundance during the 1950's even under the assumption of increased fishing mortality.

In the following sections, we examine the possible effect of water temperature on herring abundance using several alternative indices of abundance. Where possible, we have also considered the effect of parental stock size on subsequent recruitment and abundance.

Abundance Estimates Based on Sardine Production (1915–67)

Landings information along the Maine coast exists without interruption since 1937 and incomplete data are available since 1897. Although recent landings of herring along the Maine coast have been used successfully as an indication of abundance (Anthony 1972), quantities of herring landed 50 yr ago or before may be less reliable. During years of high abundance, for example, the reported landings are known to be underestimated and not proportional to abundance due to limited markets. A more accurate indication of numbers caught in the early years may be the number of cases of sardines that were actually packed. The records of cases packed per year is very accurate due to legal requirements and provide a good indication of the amount of young herring purchased by the sardine plants.

TABLE 2. Total Maine herring catch (t) by age.

Year	Age 1	2	3	4	5	6	7	8	8+	Total
1947	1 369	32 501	31 616							65 486
1948	4 342	27 441	44 654							76 437
1949	11 993	29 915	32 121							74 029
1950	281	30 644	59 632							90 557
1951	18 017	8 049	8 345							34 411
1952	5 358	44 618	29 163							79 139
1953	20 033	18 271	20 033							58 337
1954	6 067	19 970	38 030							64 067
1955	8 714	19 238	15 554							43 506
1956	5 293	33 307	27 894							66 494
1957	3 218	43 802	21 603							68 623
1958	4 498	36 592	39 669							80 759
1959	2 238	15 805	34 994							53 037
1960	950	37 864	20 534							59 348
1961	2 703	14 575	6 853							24 131
1962	624	64 520	4 232							69 376
1963	736	17 928	48 231							66 895
1964	1 209	16 645	4 023	4155	263					26 295
1965	386	25 944	3 156	183	266					29 935
1966	265	8 532	11 705	467	460	154	42	8		21 633
1967	83	8 156	12 654	4582	528	349	69	34	6	26 461
1968	92	16 279	9 034	1055	481					26 941
1969	81	6 569	15 411	783	49	45	23	7		22 968
1970	30	7 710	5 294	1712	253	292	74	69	7	15 441
1971	1 442	2 007	2 000	2651	1868	1001	437	344	346	12 096
1972	24	16 905	1 035	616	248	383	291			19 502
1973	173	7 784	7 733	234	146	85	117	84	18	16 374
1974	466	9 080	5 258	3933	262	86	32	19	4	19 140
1975	639	9 299	3 019	880	1176	72	46	35	16	15 182
1976	441	13 804	12 951	1190	860	904	14	5	20	30 189
1977	1 330	18 950	6 668	2382	615	515	1826	21	49	32 356
1978	643	12 751	7 291	1730	2910	364	709	3017	211	29 626
1979	27	25 839	11 485	1708	191	329	196	104	179	40 058
1980	1 012	9 051	26 538	8606	442	24	101		133	45 907
1981	120	39 575	1 627	2586	3815	366	20	20	120	48 249
1982	451	13 311	3 416	328	4115	2045	194	18	135	24 007

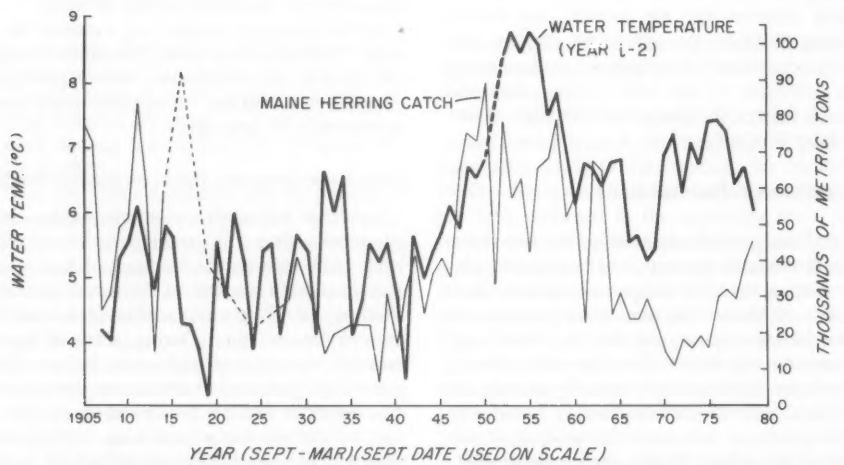

FIG. 3. Average water temperatures at Boothbay Harbor (Welch 1982), and catches of herring in the Maine juvenile fishery.

Information on the number of cases packed also extends back to 1915 without interruption. These "sardine" production figures also provide a different index of abundance than that provided by the Maine landings, since imports from New Brunswick waters are included. Anthony (1972) provided a method of estimating approximate size and age composition of the landings from 1947 to 1961 based on the number of fish packed per can. The number of cases packed in the early years, therefore, may produce a more reliable indication of abundance than the reported landings and provides data over a longer period of years. These data are given in Table 3.

To the extent that these production estimates reflect herring abundance, we may examine the possible effects of temperature and spawning stock on recruitment (Fig. 4). Assuming estimates of sardine production to be a reflection of recruitment, an index of spawning stock size may also be given by production 4 yr previously. Prior to the time of heavy fishing (when density effects on maturity became important) few age 3 fish were mature but most age 4 fish were (Anthony and Waring 1980b). Since sardine production primarily reflects age 2 abundance, then the survivors from the juvenile herring fishery will recruit to the spawning stock 2 yr later, and their progeny will recruit to the fishery after an additional 2 yr. We examined correlations between sardine production in a given year (index of recruitment) and production 3–5 yr earlier (index of spawning stock) for the period 1915–67 (excluding the war years 1941–45 when production was altered). A significant relationship was found at a lag of 4 yr ($r = 0.66$; $p < 0.01$), while lags at 3 and 5 yr were not significant. This analysis implicitly assumes that age 4 fish are the dominant component of the spawning stock.

We partitioned the recruitment index into three levels (<1.5 million, 1.5–2.5 million, and >2.5 million cases) and computed the mean seawater temperature at Boothbay Harbor (Welch 1982) during September–March 2 yr previously for each level (Fig. 4). Mean temperature for the high recruitment level (2.5 million cases) was 6.7°C, while that for the low level (<1.5 million cases) was 5.8°C (Fig. 4). It should be noted that the high recruitment period was characterized not only by higher temperature during the larval development phase but was produced by higher spawning stock levels. It is extremely difficult to separate the relative importance of temperature and spawning stock effects. For those years when recruitment was >2.5 million, from 1.5 to 2.5 million, and <1.5 million cases the average number of cases produced 4 yr earlier was 3.1 million, 1.9 million, and 1.2 million, respectively. Despite the fact that these indices of recruitment and spawning stock are relatively crude, there does appear to be a qualitative relationship between stock and recruitment, which, in turn, appears to be influenced by temperature. This simple analysis assumes a proportional relationship between indices of spawning stock and recruitment and does not consider possible density-dependent effects. A more detailed analysis of stock–recruitment relationships is provided in the following sections.

TABLE 3. Number of cases of sardines packed by the Maine Sardine Industry and average seawater temperature at Boothbay Harbor, Maine, from September to March (year $i + 2$ refers to year in which September occurs).

Year i	No. of cases packed (1000's)	Average water temperature over September to March (°C) (year $i + 2$)
1915	2446	3.2
1916	2268	5.6
1917	2489	4.7
1918	2458	6.0
1919	2550	5.2
1920	1986	3.9
1921	1400	5.4
1922	1870	5.5
1923	1272	4.1
1924	1900	4.9
1925	1870	5.7
1926	1718	5.4
1927	1262	4.1
1928	2056	6.6
1929	2026	6.0
1930	1399	6.6
1931	885	4.1
1932	546	4.6
1933	981	5.6
1934	1143	5.2
1935	1656	5.6
1936	1846	4.7
1937	1680	3.5
1938	672	5.7
1939	2210	5.0
1940	1118	5.4
1941	3165	5.7
1942	2573	6.1
1943	2505	5.8
1944	3262	6.7
1945	2725	6.6
1946	3276	6.8
1947	3014	7.7
1948	3682	8.4
1949	3075	8.8
1950	3844	8.4
1951	1677	8.8
1952	3531	8.6
1953	2782	7.4
1954	2935	7.9
1955	1269	7.1
1956	2231	6.1
1957	2218	6.8
1958	2100	6.7
1959	1753	6.4
1960	1998	6.8
1961	754	6.8
1962	2144	5.5
1963	1637	5.6

Abundance Estimates Based on Catch-Per-Unit and Virtual Population Analysis (1951–79)

In an attempt to circumvent the difficulties associated with using landings or production statistics as indices of abundance, we have assembled several independent measures of abundance based on standardized catch-per-unit-effort (CPUE) and calibrated these values using population size estimates derived from VPA (Gulland 1965a). Fogarty and Anthony (1982) provided VPA abundance estimates for the western Gulf of Maine region (combined catches of the coastal Maine juvenile herring fishery and the western Gulf of Maine adult herring fishery) for the period 1965–81. A detailed explanation of data sources and analytical procedures, including determination of terminal fishing mortality rates, is given in Fogarty and Anthony (1982).

To examine stock and recruitment for the period of changing water temperatures in the late 1940's and early 1950's, indices

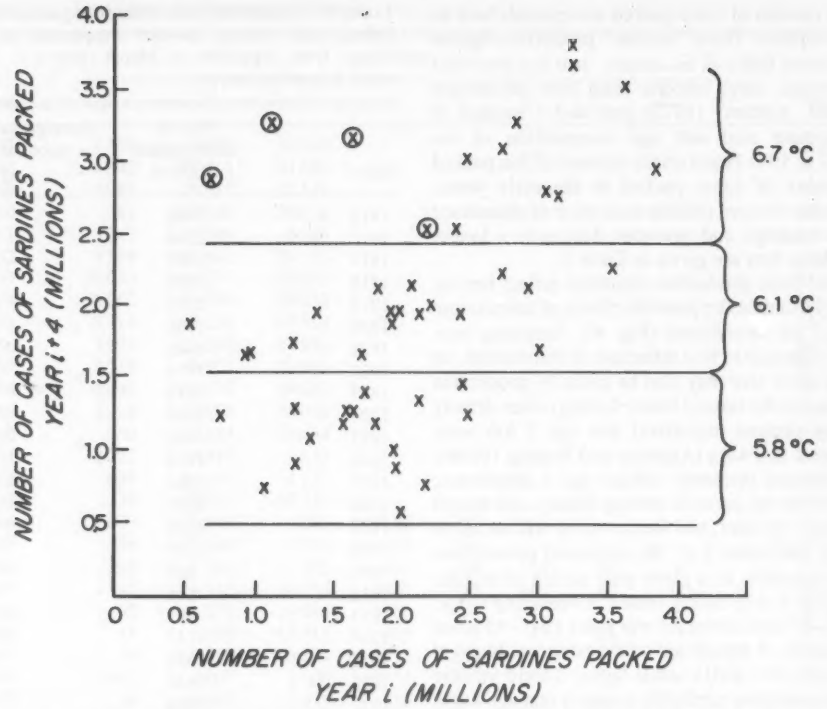

FIG. 4. Number of cases of sardines packed along the Maine coast from 1915 to 1967 plotted against the cases packed 4 yr earlier (World War II years are circled). Water temperature is shown averaged over September–March in year of birth ($i + 2$).

of abundance had to be estimated prior to 1965. The VPA from 1965 to 1981 was extended back to 1962 using the Maine sardine fishery catches and assuming that no other catches occurred. These population size estimates provided the basis for calibrating relative abundance indices for earlier periods.

For the years 1960 and 1961, indices of age 2 abundance were taken from CPUE values averaged on a weekly basis by sections of the Maine coast as derived by Anthony (1971). The index consisted of the mean weekly CPUE averaged over a specified period during the peak of the fishing season adjusted for changes in vulnerability due to moon phase effects (see Vulnerability section). These relative indices of abundance at age 2 overlapped the virtual population time series for the years 1962 to 1965 and agreed very closely with the VPA estimates in terms of relative abundance. The ratio of relative abundance (CPUE) for the 1960 year class at age 2 to the corresponding VPA abundance estimate was used to raise the CPUE estimates for the 1958 and 1959 year classes at age 2 to estimates of absolute abundance.

Anthony (1972) also examined standardized fishing effort for a selected group of stop seine fishermen in central and western Maine for the period 1951–70 (see also Anthony and Waring 1980a). Fishing power coefficients and density indices were calculated by the method of Robson (1966) to obtain abundance indices (ages 1–3). Relative density indices for western and central Maine were averaged for each year with the total catch per stop seine values after being standardized against the 1960 year class at age 2. The ratio of this standardized abundance index to the corresponding VPA estimates (ages 1–3 combined) for 1962 provided the basis for raising the abundance index to total numbers for the period 1951–59. An evaluation of the possible error introduced by this procedure was made by comparing the raised CPUE estimates for 1963–70 to the actual VPA estimates. The mean absolute error was 22% during 1963–70 but only 14% for 1964–69. We assumed this to be an acceptable level of error and applied this method to the years 1951–59. This method provides estimates of abundance for ages 1, 2, and 3 combined. To estimate the abundance of age 2 herring, an average percentage reduction was taken from the average portion of age 2 herring of age 1–3 as derived from VPA over the years 1962–70.

Estimates of abundance of age 2 herring found along the Maine coast were thus derived from a VPA for the years 1962–80, from mean weekly CPUE for the years 1960 and 1961, and from least squares estimates of density (Robson 1966) and annual CPUE for the years 1951–59 (Table 4).

Herring catch-at-age data are available from 1947 (Table 2) but no estimates of abundance are available prior to 1951. Anthony (1972, p. 148, fig. 25) showed that herring catches from central and western Maine in themselves were reliable predictors of abundance. To obtain a rough estimate of age 2 abundance from 1947 to 1950, therefore, the catch at age 2 was plotted against the estimated age 2 abundance for the years 1951–58 and estimates of abundance were taken off a freehand curve. Although the resulting estimates of age 2 abundance from 1947 to 1950 are only approximate, they are very useful, since it is known that these year classes were very abundant and similar to those of the 1950's. These estimates are also provided in Table 4.

Using the catch information given in Table 2, age 1 estimates

TABLE 4. Estimates of abundance used to examine stock–recruitment relationships with temperature.

Year	Abundance (millions) at age: 1	2	3	4	5	Abundance (t) at age:[a] 4	5	Total
1947	3146	2480						
1948	3330	2480	1060					
1949	4208	2350	1039	499				
1950	1119	2580	1088	618	409	111.2	90.0	201.2
1951	4284	888	940	294	506	52.9	111.3	164.2
1952	3011	2215	487	703	241	126.5	53.0	180.0
1953	4542	2066	494	174	576	31.3	126.7	158.0
1954	2910	2205	1145	248	142	44.6	31.2	75.9
1955	4360	1789	1095	569	203	102.4	44.7	147.0
1956	3434	2930	934	787	466	141.7	102.5	244.2
1957	3894	2319	1290	523	644	94.1	141.7	235.8
1958	3178	2929	566	882	428	158.8	94.2	252.9
1959	2610	2227	1179	119	722	21.4	158.8	180.3
1960	1086	1929	1210	628	97	113.0	21.3	134.4
1961	4431	538	306	811	514	146.0	113.1	259.1
1962	1658	3420	99	213	664	38.3	146.1	184.4
1963	1248	1310	818	53	174	9.5	38.3	47.8
1964	2141	955	387	234	43	42.1	9.5	51.6
1965	969	1664	365	293	171	52.7	37.6	90.4
1966	1032	757	533	247	238	44.5	52.4	96.8
1967	2046	826	358	250	200	45.0	44.0	89.0
1968	662	1656	436	184	171	33.1	37.6	70.7
1969	484	535	574	205	129	36.9	28.4	65.3
1970	226	391	243	218	145	39.2	31.9	71.1
1971	1781	183	154	149	145	26.8	31.9	58.7
1972	491	1360	94	87	81	15.7	17.8	33.5
1973	435	410	790	56	31	10.1	6.8	16.9
1974	758	346	196	561	39	101.0	8.6	109.6
1975	689	593	120	101	360	18.2	79.2	97.4
1976	902	532	330	60	59	10.8	13.0	23.8
1977	1412	716	160	150	31	27.0	6.8	33.8
1978	1945	1087	203	58	81	10.4	17.8	28.3
1979	440	1547	596	91	29			

[a]Mean weights of age 4 herring assumed to be 0.18 kg. Mean weights of age 5 herring assumed to be 0.22 kg.

of abundance were calculated (recruitment at January 1) from the estimates of abundance at age 2. The catches at age 2 and 3 were then used to calculate estimates of abundance at ages 3, 4, and 5 for year classes 1945–58 (Table 4). Estimates of abundance for the 1959–75 year classes were taken from VPA estimates (Fogarty and Anthony 1982).

The biomass at ages 4 and 5 from Table 4 was assumed to be a satisfactory index of spawning stock biomass, and this was plotted against the recruitment at age 1 (from Table 4) in Fig. 5. Estimates of total spawning biomass were not made because forward projection estimates of abundance are not reliable for more than a few ages.

Stock–recruitment curves were fitted to the data for two time periods according to the method of Shepherd (1982). A slope at the origin was determined by allowing 10% of the data to fall on or left of the slope, and representative points through the bulk of the data were arbitrarily chosen to ensure that the curve passed through the center of each data set. Clearly, this estimation procedure is subjective, but may be as reliable as formal statistical methods, given the limitations of the data. Both curves have the same slope at the origin which defines the maximum recruitment per unit biomass and represents the recruitment level that would be attainable in the absence of density-dependent effects. The stock–recruitment relationship proposed by Shepherd is

$$R = \frac{\alpha B}{1 + (B/K)^{\beta}}$$

where K is the threshold biomass which measures the biomass above which density-dependent effects dominate, α is the slope at the origin, β is a shape parameter (degree of compensation), here set equal to 1 for the Beverton and Holt curve, and R and B are the estimated recruitment and parental stock levels, respectively. As the spawning stock biomass declines toward the slope at the origin (Fig. 5), density-dependent processes become less effective. Except for the 1960 year class the upper curve passes through nine data points, which describe conditions under unusually high water temperatures just after spawning (September–March), averaging 7.9°C. The lower stock–recruitment curve passes through 19 data points, which are representative of temperature conditions averaging 6.5°C (Fig. 5). These two stock–recruitment curves suggest two relationships of recruit-

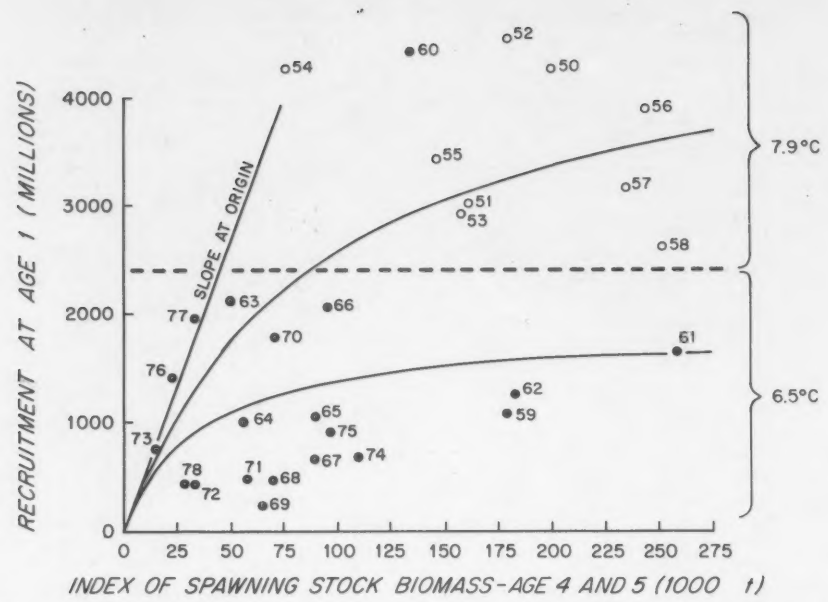

FIG. 5. Stock–recruitment curves for two time periods for Gulf of Maine herring. The temperatures are average surface water temperatures at Boothbay Harbor over September–March in the year of birth.

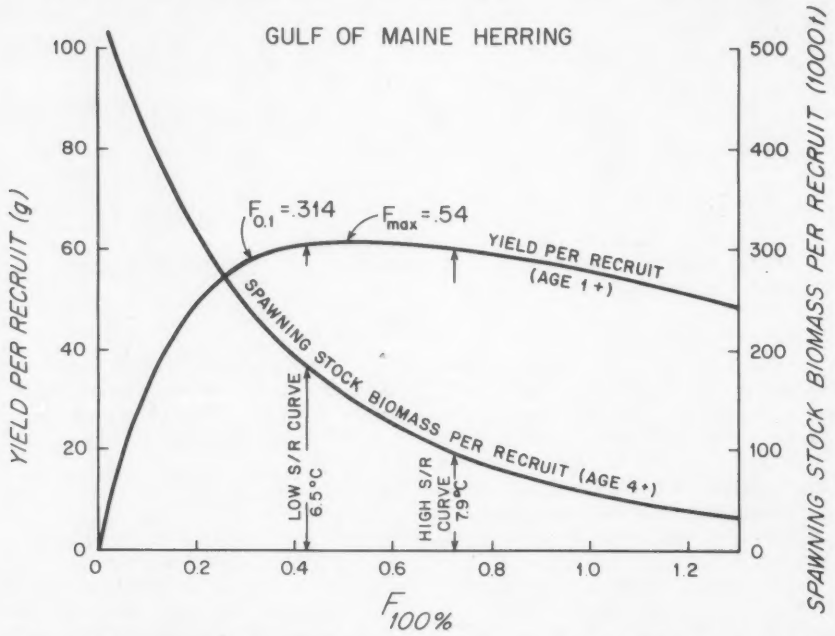

FIG. 6. Yield per recruit and spawning biomass per recruit curves for Gulf of Maine herring showing the relationship of two productivity levels.

ment for various spawning stock biomass levels as a function of temperature.

Yield per recruit and spawning stock biomass per recruit curves are provided in Fig. 6. These curves were derived using recent growth information and exploitation patterns, however, which may not apply for earlier years. An important implication of the possibility of different stock–recruitment relationships under different environmental conditions is that the stock may withstand differing levels of fishing mortality. Two points are indicated on the two curves in Fig. 6 that are representative of the high and low stock–recruitment relationships. Under the higher stock–recruitment relationship, a fishing mortality rate

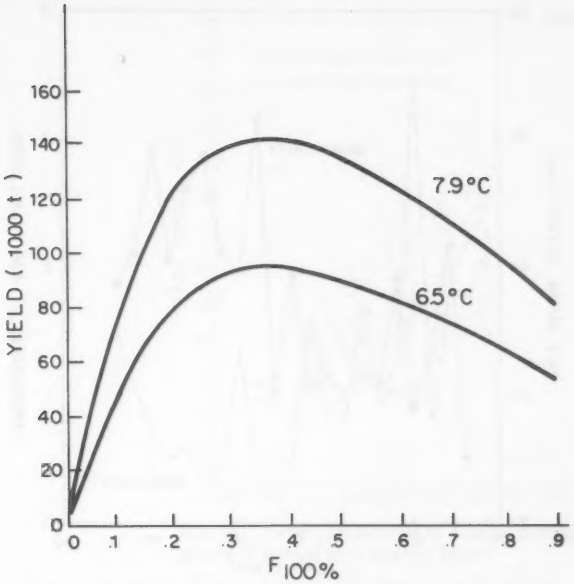

FIG. 7. Sustainable yield as a function of fishing mortality (F) and September–March water temperatures for the Gulf of Maine herring.

of about 0.7 would be comparable with a fishing mortality rate of about 0.4 under the lower stock–recruitment curve (i.e. the stock could withstand higher levels of fishing mortality with the same probability of stock collapse). Sustainable yields (product of yield-per-recruit and recruitment at a given fishing mortality rate) under the two stock–recruitment curves characteristic of the differing temperature regimes are provided in Fig. 7.

Abundance Estimates Based on Virtual Population Analysis (1965–81)

Detailed sampling of the age composition of herring fisheries within the Gulf of Maine since 1965 provided the basis for population size estimates using VPA (Gulland 1965a). Fogarty and Anthony (1982) described the data base and method of analysis for these estimates. We examined the relationship between abundance at age 2 (age of full recruitment to the juvenile herring fishery) as estimated using VPA and seawater temperature at Boothbay Harbor (Welch 1982) for the 1965–79 year classes. A preliminary analysis (V. C. Anthony and M. J. Fogarty, unpubl. data) indicated that no significant effects of salinity, sea level, and Ekman transport could be demonstrated. Accordingly, only temperature-related effects are considered in the present analysis. We partitioned the annual temperature data into three periods corresponding to several early life history stages: (1) September–December (egg and early larval development), (2) January–April (overwintering – late larval period), and (3) May–August (early juvenile phase). For each period, the mean, minimum, and maximum monthly temperatures were computed and correlated with recruitment estimates based on VPA. Temperature values used in the analysis corresponded to the first year of life for the 1965–79 year classes. Correlation coefficients between recruitment and the temperature variables for each period are provided in Table 5. Significant correlation coefficients ($p < 0.05$) were noted for the mean and minimum temperatures during January–April and the minimum monthly

TABLE 5. Correlation coefficients between herring abundance at age 2 determined by virtual population analysis and the minimum, mean, and maximum water temperatures during the first year of life (*Significant at $p < 0.05$, df = 13).

	Period		
Temperature	September–December	January–April	May–August
Minimum	−0.15	−0.61*	−0.62*
Mean	−0.14	−0.54*	−0.49
Maximum	−0.37	−0.38	−0.23

temperature during May–August (Table 5). These analyses indicated an inverse relationship between temperature and recruitment, in distinct contrast with inferences drawn from earlier time periods, particularly during the 1950's when an apparent direct relationship between temperature and yield was noted. A multiple regression of recruitment on the minimum water temperatures for the January–April and May–August periods was significant ($p < 0.02$), with a multiple correlation of 0.70. The derived equation was

$$R = 3083.7 - 223.6T_1 - 226.1T_2$$

where R is recruitment at age 2, T_1 is the minimum January–April temperature, and T_2 is the minimum May–August temperature. An examination of the residuals provided no indication of autocorrelation. Due to the high correlation between the mean and minimum January–April temperatures, no attempt was made to incorporate the former into the model. These results indicate that the late larval – early juvenile period may be most critical in the establishment of year class strength.

Comparison of minimum winter temperatures with larval mortality during winter (Graham 1982) for the 1964–73 year classes indicated that mortality was greater with higher minimum winter temperatures (Fig. 8). A marked exception was observed for the 1964 year class, which experienced extremely low minimum winter temperatures (0.1°C) but also high mortality. It is conceivable that mortality increases sharply when temperatures decline to some threshold value (~0.°C). Chenoweth (1970) and Graham and Davis (1971) attributed low abundance of the 1964 year class to abnormally low winter temperatures. These observations suggest that the regression equation developed above may require modification to account for extremely low temperatures.

Inverse correlations between herring year class strength and temperature have been noted by Postuma and Zijilstra (1974) in the North Sea and Bowers and Brand (1973) in the North Irish Sea.

Growth and Its Relation to Abundance and Temperature

Although recruitment is the dominant component of production for Gulf of Maine herring, changes in growth in relation to environmental factors and population size are of particular interest. In this section, we examine the relationship between growth rate and water temperature and abundance.

Mean length at age 2 was regressed on temperature and abundance in an attempt to evaluate both density-independent and density-dependent influences on growth. Mean length at age 2 was considered to reflect early growth history of the cohort although growth rate per se was not addressed. Mean length at age for western Maine herring in October was employed in subsequent analyses. An index of temperature during the period

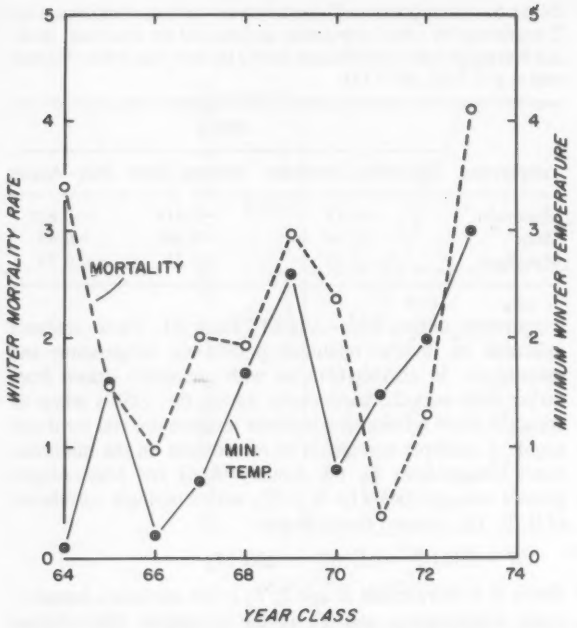

FIG. 8. Relationship between the instantaneous winter mortality rate of larval herring (Graham 1982) and minimum monthly water temperature at Boothbay Harbor for the 1964–73 year classes.

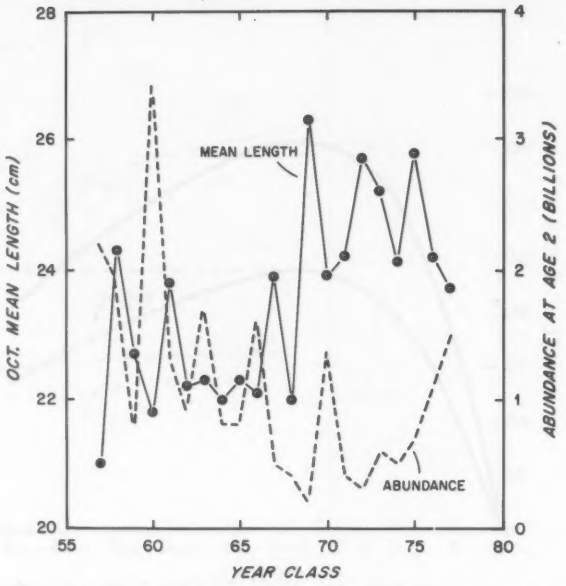

FIG. 9. Comparison of Atlantic herring abundance at age 2 with mean length in October at age 2.

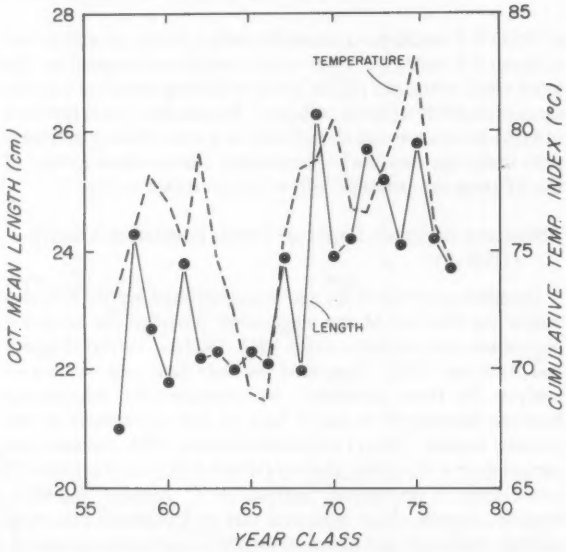

FIG. 10. Comparison of cumulative water temperature during June–October of the first growing season with mean length in October at age 2.

when most growth occurs, June–October, was derived by taking the cumulative mean monthly surface water-temperature at Boothbay Harbor (Welch 1982) during this period. Abundance at age 2 was determined by VPA (Fogarty and Anthony 1982).

Multiple linear regression analyses of mean length at age 2 on cumulative temperature during the first and second growth periods (i.e. June–October during the first and second years of life) and abundance indicated that both temperature during the first growing season and abundance at age 2 were significantly related to mean length at age 2 (Table 6; Fig. 9 and 10). Mean length at age was inversely related to year class strength (Fig. 9) but positively related to temperature during the first growing season (Fig. 10). Temperature-related effects on growth have also been noted by Day (1957), Burd (1962), and Moores and Winters (1982). Sinclair et al. (1982b) found no clear evidence of temperature effects on yield but did document an apparent change in growth pattern of southwest Nova Scotia herring during the early 1970's.

Qualitatively similar results were obtained when relative growth rate, defined as

$$G = \log_e (l_2/l_0)\Delta t$$

where l_2 is the October mean length at age 2, l_0 is the assumed length at October 1 in the year of hatching (arbitrarily set at 1 cm), and t is time in months, was employed. This is to be expected, since G is monotonically related to l_2.

Additional analyses relating relative growth rate during the second growth period, i.e.

$$G = \log_e (l_2/l_1)\Delta t$$

TABLE 6. Coefficients and significance levels for multiple regression analysis of temperature and density effects on mean length at age 2 for the 1958–79 cohorts ($R = 0.75$). Temp 1 = cumulative mean temperature during June–October of first growth season; Temp 2 = cumulative mean temperature during June–October of second growth season; Abund 2 = abundance at age 2.

Variable	Coefficient	T	p
Temp 1	0.412	2.390	0.028
Temp 2	0.166	0.976	NS
Abund 2	−0.452	−2.823	0.0113

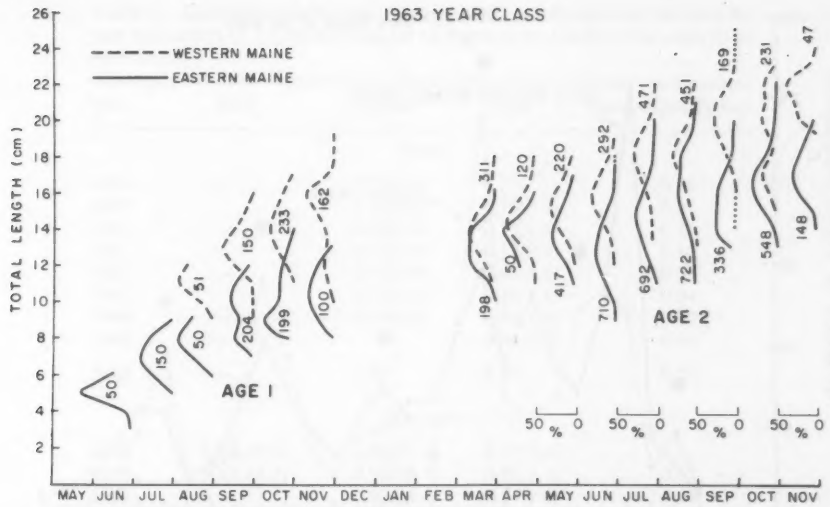
1963 YEAR CLASS
WESTERN MAINE
EASTERN MAINE
TOTAL LENGTH (cm)
AGE 1
AGE 2
50 % 0
MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV

FIG. 11. Length frequencies of Atlantic herring from western and eastern Maine indicating the faster growth of herring from western Maine.

where l_1 is the mean length during June at the start of the second season and l_2 is the mean length during October, to June–October temperature during that year indicated no significant ($p > 0.05$) temperature or density effects.

These results imply that environmentally induced differences in growth rate of juvenile herring during the first year of life determine differences in size attained by the cohort at least through age 2.

Anthony (1971) demonstrated growth differences among sections of the Maine coast. Herring from western Maine grow faster through age 2 than do herring from eastern Maine for all year classes and at the end of age 2 are on average nearly 3 cm longer (Fig. 11). This may be because environmental conditions in eastern Maine differ substantially from central or western Maine. Sherman (1965, 1966, 1968) demonstrated large differences in zooplankton density during the summer. For 1963–65, the mean volume of zooplankton (cubic centimetres per 100 m^3 of water) was 11.0, 11.0, and 42.3, respectively, in western Maine compared with 1.2, 1.6, and 0.4, respectively, in eastern Maine. Surface water temperatures, from 1922 through 1962, averaged 6.9°C annually at St. Andrews in Passamaquoddy Bay, New Brunswick (Lauzier and Hull 1962; and pers. comm.), and 8.4°C at Boothbay Harbor in western Maine. Sherman (1965, 1966, 1968) gave salinity profiles from an offshore–inshore transect for the summers of 1963, 1964, and 1965 that show surface salinities of 31.7–32.4‰ in eastern Maine as compared with 31.3–31.7‰ for western Maine. Growth of herring in eastern Maine has been consistently slower than in western Maine since records have been kept.

Evidence for density-dependent changes in length at age 2 was evident only when the strong year classes observed during the latter 1950's – early 1960's were included in the analysis. Anthony (1971) had earlier demonstrated a density-dependent effect for the 1959–63 year classes. When the 1965–79 year classes only were considered, no significant ($p > 0.05$) density effect could be demonstrated and the relationship between temperature and mean length at age was more clearly defined (Table 7; Fig. 10). Sinclair et al. (1982b) found some evidence of density-dependent inhibition of growth for southwest Nova Scotia herring after correction for an apparent growth discontinuity. Similarly, Moores and Winters (1982) reported a weak density-dependent effect on growth of herring in Fortune Bay, Newfoundland.

TABLE 7. Coefficients and significance levels for multiple regression analysis of temperature and density effects on mean length at age 2 for the 1965–79 cohorts ($R = 0.78$). Temp 1 = cumulative mean temperature during June–October of first growth season; Temp 2 = cumulative mean temperature during June–October of second growth season; Abund 2 = abundance at age 2.

Variable	Coefficient	T	p
Temp 1	0.753	3.474	0.005
Temp 2	0.109	0.530	NS
Abund 2	0.002	0.297	NS

Growth is related to both abundance at age 2 and summer water temperature (Fig. 10 and 11). When abundance is high, however, growth is slow regardless of temperature. Density-dependent effects appear to dominate temperature-related factors in determining growth rates.

Vulnerability of Herring Due to the Phase of the Moon

The catch of juvenile herring along the coast of Maine varies not only with abundance but also due to changes in availability and vulnerability to the traditional fixed gear fishery. In certain years, for as yet unknown reasons, young herring remain offshore away from the coves and islands where stop seines and weirs operate. Movement of young herring inshore increases their availability to fixed gear, and the physical environment, in particular the phase of the moon, affects their vulnerability.

The dependence of the Maine herring catch on the phase of the moon can be marked. For example, in 1961 the abundance of herring was very low, yet Maine fishermen took advantage of the dark phases of the moon to compensate (Fig. 12). The relationship of catches with moon phase was less pronounced in

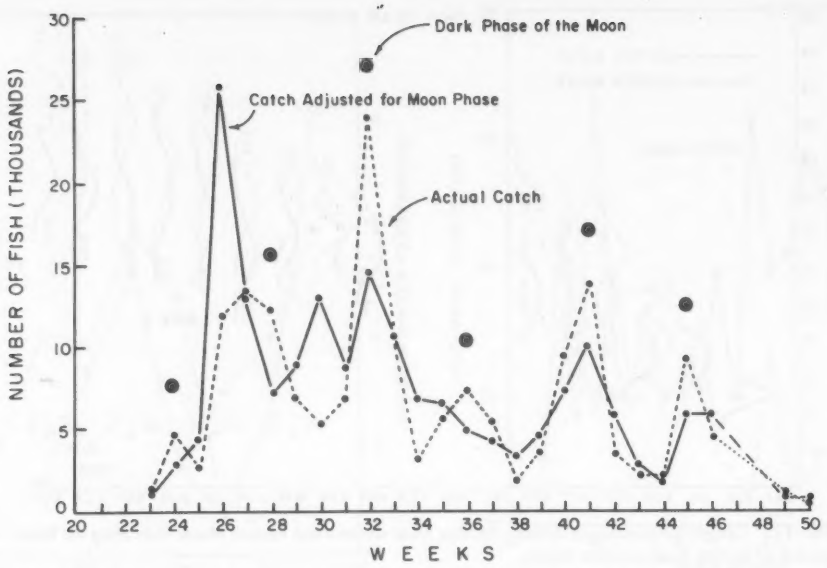

FIG. 12. An example of increase in herring catch during the dark phase of the moon and the subsequent adjustment of the data (western Maine, 1961).

other years and areas but the effect is prominent in all areas for both stop seines and weirs.

To determine the effect of the moon phase on herring catches, correlation coefficients were calculated between herring catches and moon phase for each gear, section of the Maine coast, and year (Table 8). There is an obvious difference in the effect of the moon phase on catches by gear and area along the Maine and New Brunswick coasts. The correlation coefficient of stop seine catches with the phase of the moon was 0.92 for the years 1958–65 for both western and central Maine but only 0.73 for eastern Maine and 0.67 for Passamaquoddy Bay. Weir coefficients were somewhat lower (0.67, 0.50, and 0.70 for central Maine, eastern Maine, and Passamaquoddy Bay, respectively). The herring catch is more dependent on the phase of the moon in western Maine than in eastern Maine and with stop seines than with weirs. The correlation of moon phase with catch was also greatest when the annual catch was low (Table 8). In eastern Maine the reverse was true. The western Maine coast has deeper water closer to shore than eastern Maine. Herring can, therefore, be relatively close inshore in western Maine and still not be very vulnerable to capture. When fish are abundant, however, there are enough deep coves that can be shut off by stop seines in western Maine to provide a reasonable catch. When herring are scarce, only a few coves may contain fish and some of these may only be shut off if the fish are well inside, an effect that is most pronounced during the dark phase of the moon.

Since stop seines are somewhat mobile, there is also more effort directed toward the taking of herring during the dark phase of the moon when herring are scarce. In eastern Maine where fixed weirs (traps) predominate, herring must be in shallow water for the weirs to be effective. The effectiveness of the weirs is altered by factors causing herring to move inshore and also by increased vulnerability during the dark phase of the moon. Weirs are slightly more effective during the dark phase of the moon and catches are greater when herring are most plentiful (available).

Discussion

Environmental effects on productivity of exploited marine fish stocks have been extensively documented (Cushing 1982). The relationships between temperature and yield and/or abundance have been examined in considerable detail, undoubtedly due to the ready availability of temperature and catch records. It should be stressed, however, that the effect of temperature on fish populations may be indirect rather than direct. Temperature may also be correlated with variables of greater importance (e.g. upwelling or other hydrographic features) and may therefore serve primarily as a proxy variable. We have examined the importance of temperature mediated effects on recruitment, growth, and vulnerability of Atlantic herring in the Gulf of Maine region. An attempt has been made to construct population size estimates for an extensive period based on several alternative indices of abundance and to relate these estimates to environmental variables, particularly temperature. It is recognized that the use of landings statistics or other measures of commercial production as indices of stock size are subject to error, since numerous factors (economic, physical, and biological) affect fishery yields. Landings statistics are an adequate index of abundance only if availability and fishing mortality are relatively constant. Of particular concern in the present analysis is the separation of changes in availability from changes in abundance levels. We noted sharply increased herring landings during the 1950's; this period was also characterized by high temperature levels. Although herring recruitment and growth may have been enhanced during this period (e.g. due to increased overall productivity) it is also possible that juvenile herring were more available to the inshore fisheries. Sherman et al. (1982) reported that the abundance and species composition of zooplankton assemblages have not undergone large-scale changes, presumably eliminating changes in productivity of lower trophic levels as a possible explanation of increased herring abundance. Since these fisheries are primarily

TABLE 8. Correlation coefficients of herring catch with the phase of the moon by year and section of the Maine coast for each gear type. Catches of all ages (t) in parentheses.

Year	West	Central	East	Passamaquoddy Bay
		Weirs		
1958	—	0.74(1.4)	0.22(7.1)	0.75
1959	—	0.21(0.6)	0.79(2.9)	0.31
1960	—	0.58(1.4)	0.13(4.6)	0.23
1961	—	0.77(0.5)	−0.52(0.8)	0.16
1962	—	−0.36(0.8)	0.96(4.6)	0.65
1963	—	0.03(0.8)	0.18(2.8)	0.04
1964	—	0.54(0.6)	0.50(1.4)	0.70
1965	—	—	0.44(5.8)	0.73
Total	—	0.67	0.50	0.70
		Stop seine		
1958	0.80(30.9)	0.68(27.1)	0.27(7.0)	—
1959	0.43(24.2)	0.96(16.3)	0.88(4.5)	0.67
1960	0.91(17.3)	0.97(24.0)	0.54(2.6)	0.69
1961	0.98(8.8)	0.48(6.0)	0.31(0.9)	0.06
1962	0.33(24.7)	0.15(23.0)	0.31(3.2)	0.11
1963	0.69(15.3)	0.68(23.5)	0.84(3.2)	—
1964	0.89(11.3)	0.55(6.9)	−0.01(1.8)	0.47
1965	0.67(6.9)	0.44(10.8)	—	—
Total	0.92	0.92	0.73	0.67
		Purse seine		
1958	—	—		—
1959	—	—		−0.31
1960	—	—		−0.24
1961	0.36(2.8)	0.68(2.3)		0.13
1962	0.41(1.4)	0.04(1.3)		0.60
1963	−0.39(0.8)	0.18(0.3)		−0.00
1964	−0.21(1.3)	0.17(1.6)		−0.22
1965	0.03(1.8)	—		−0.33
Total	0.07	0.44		−0.52

prosecuted using passive (fixed) gear, catch levels depend strongly on the behavior (migratory patterns, activity, and feeding levels) of the fish. It is conceivable that herring from the Georges Bank and Nantucket Shoals regions, for example, moved northward during the period of warmer temperatures and were, therefore, vulnerable to the coastal Maine fisheries. Spawning stocks of herring in the southwestern Gulf of Maine are at the southern extent of the range and it is possible that thermal preferences would result in a northward shift during warmer periods. Given the available data, it is not possible to determine if increased catches were due to increased abundance of availability, and potential explanations must remain speculative.

In contrast with the results of long-term analyses of herring abundance and yield versus temperature, a more detailed examination of the relationship between year class strength for the 1965–79 cohorts and temperature suggested an inverse correlation. Cushing (1982) noted that inverse relationships between temperature And year class strength may reflect delayed development, resulting in enhanced synchrony between larval development and prey availability. This hypothesis offers a plausible explanation for our observations. Within the Gulf of Maine, dominant copepod prey of larval herring (nauplii and copepodites of *Pseudocalanus minutus*, *Oithona* spp., and *Acartia* spp. and *Calanus finnemarchicus*) decline to an annual minimum during January–February and peak during July–August (Sherman et al. 1976). *Pseudocalanus minutus*, an important prey item of larval herring, peaks in abundance during September–October (Sherman et al. 1976) and is apparently readily available during early larval herring development. The winter minimum of copepod production, however, does suggest a critical food-limited period. Decreased water temperature during winter and a concomitant delay in larval herring development would possibly result in correspondence with copepod production, particularly with *Calanus*, which peaks in abundance during March–April, and *Pseudocalanus*, which reaches peak abundance slightly later (Sherman et al. 1976). This explanation is somewhat simplistic, since it would seem probable that natural selection would favor synchrony between larval production and food availability, and therefore this correspondence should not be unusual.

Cohen and Lough (1983) noted a shift in the diet of Atlantic herring from the 1974–75 winter period to the 1975–76 and 1976–77 winter periods. During the 1974–75 season *Centropages* spp. and *Pseudocalanus* sp. dominated the larval diet; during the 1975 and 1976 periods *Pseudocalanus* sp. and

Paracalanus parvus were dominant. Larvae during the winter of 1976 were more robust than larvae in the previous two years and Lough et al. (1981) indicated that the autumn–winter mortality in the 1976–77 period was the lowest for the three year classes. Cohen and Lough (1983) speculated that increased survival of herring larvae during the 1976 spawning season would result from a switch in diet and an increase in relative population levels of the copepod prey *Pseudocalanus* and *Paracalanus*.

Our results further suggest that temperature-related effects are more important in the late larval – early juvenile phase than in the early larval period. Sissenwine et al. (1984) came to a similar conclusion based on an analysis of mortality rates for early life history stages of several species including Atlantic herring. Sissenwine et al. (1984) stressed the potential importance of predation on late larval – early juvenile stages. Temperature could have affected the distribution or abundance of herring predators and therefore had a secondary effect on herring year class strength. There is currently little evidence of the widespread importance of starvation of larvae in the Northwest Atlantic (G. Lawrence, NOAA, NMFS, Narragansett, RI, pers. comm.), suggesting that predation is indeed more important. The predation hypothesis may be considered an alternative to the match–mismatch thesis; however, its relationship with temperature is unknown.

Discrepancies in the apparent relationship between temperature and herring abundance for different time periods have been noted previously. Skud (1982) reported that interspecific interactions with Atlantic mackerel also affect herring abundance levels. Skud (1982) examined the historical herring–mackerel interaction based on recorded catch statistics and reports of catches dating back to the early 1800's and attempted to relate this interaction to environmental factors. He noted that during much of the 1800's mackerel were more abundant than herring. Following a collapse of the mackerel fishery in the late 1880's, herring became more abundant, declined in the 1930's, and greatly increased in abundance during the 1940's and 1950's. He noted that herring abundance was positively correlated with temperature when herring were more abundant than mackerel, but negatively when mackerel were more abundant or when the population was shifting. This result is in agreement with the results of the present analysis. We found an inverse relationship between water temperature and recruitment during the recent period (1965–81) when mackerel were generally more abundant than herring. In the 1940's and 1950's, however, when herring were more abundant than mackerel, we found an apparent positive relationship between abundance and temperature. This observation, although intriguing, remains circumstantial, since we are unaware of any specific biological rationale to explain a relationship of this type.

Examination of correlations between time series of abundance (or yield) and environmental variables is problematical, since serial correlation in the variables of interest may result in spurious relationships (Gulland 1965b; Ricker 1975). In the present analysis, residuals of all regression analyses were checked for first-order autocorrelation by the Durbin–Watson statistic.

We have also considered environmental effects on stock–recruitment relationships for Gulf of Maine herring. The suggested relationship of stock and recruitment with temperature occurred, however, in the earlier years of the fishery when the fishing pressure was fairly constant on juvenile herring and only existed on juvenile herring in inshore areas apart from the spawning grounds. There was no fishing at all on the spawning grounds of Georges Bank, southwestern Nova Scotia, or Jeffreys Ledge at that time. Anthony and Waring (1980b) reviewed the problems of estimating levels of stock and recruitment in Gulf of Maine herring populations associated with heavy fishing. Some of these were temporal and areal changes in the fisheries coupled with intermixture of stocks during different phases of the seasonal migrations, disruption of spawning activity, difficulties in estimating the proportion of fish having spawned prior to capture, annual variability in size or age at maturity, and recruitment to the spawning grounds. These authors, in fact, suggested that the act of fishing itself on the spawning grounds may have masked any stock–recruitment relationship in recent years. Despite limitations of the data, we noted a simple proportional relationship between indices of stock size and recruitment based on sardine production for the period 1915–67. The recruitment index was highest when both stock size and temperature levels were high and thus it is not possible to clearly separate the effects of these variables. A more detailed analysis based on reconstructed abundance levels for the period 1951–79 was made using the method of Shepherd (1982). High recruitment was again apparently related to high spawning stock and temperature. To demonstrate the implications of modification of the stock–recruitment relationship by changing temperature conditions, we have constructed two curves that are representative of two different temperature regimes. This method, although subjective, provided useful insights into the capacity of the stock to withstand differing levels of fishing mortality depending on evironmental conditions.

Environmental effects were also evident on growth. Herring length at age 2 was inversely related to year class strength but positively related to temperature during the first growing season. In fact, the temperatures during the first year of life determine differences in size at least through age 2. Of the two effects, however, density is more important. Growth is slow regardless of temperature when abundance is high. Anthony (1971) showed that herring from western Maine (warm water) grew faster than herring from eastern Maine (cold water) although abundant year classes grew slower in both areas and poor year classes grew faster in both areas. Anthony and Waring (1980b) indicated that maturity of age 3 and 4 herring from Georges Bank increased greatly after 1970 when the stock abundance declined sharply. The growth increased greatly and herring continued to mature apparently according to length. These observations suggest that herring have a remarkable ability to compensate for the effects of fishing. Data for Georges Bank herring strongly suggested that fecundity was density dependent so that as the stock declined the multiplicative effects of increased growth, maturity, and fecundity produced a strong compensation in terms of the number of eggs produced. For the Georges Bank stock, for example, age 3 herring increased in length by 9% from the mid-1960's to the mid-1970's according to Anthony and Waring (1980b). They increased in maturity by 63%, in recruitment by 181%, and in fecundity at length by 129%.

Environmental effects on herring populations are complex and are often confounded with biological factors such as spawning stock size and possibly competition and predation. The mechanisms relating to temperature are poorly understood and are probably indirect. Other environmental effects (e.g.

temperature–growth relationships and moon phase effects on vulnerability) on Gulf of Maine herring are generally consistent with observations with other herring populations.

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Environmental Variation and Recruitment of Pacific Herring (*Clupea harengus pallasi*) in the Strait of Georgia[1]

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Stocker, M., V. Haist, and D. Fournier. 1985. Environmental variation and recruitment of Pacific herring (*Clupea harengus pallasi*) in the Strait of Georgia. Can. J. Fish. Aquat. Sci. 42(Suppl. 1): 174–180.

We used an age-structured model to estimate recruitment for the Strait of Georgia Pacific herring (*Clupea harengus pallasi*) population. The model used for herring is a version of the model described in Fournier and Archibald (1982. Can. J. Fish. Aquat. Sci. 39: 1195–1207), modified to include spawn survey information. Three structural assumptions are made to include the spawn data: (1) the form of the relationship between the actual spawn and the observed spawn, (2) the form of the relationship between escapement and actual spawn, and (3) the existence of a Ricker spawn–recruitment relationship, with a multiplicative environmental component. In order to determine which environmental factors had a significant effect on recruitment, we attempted to explain the residual variation from the Ricker curve with the environmental variables using exploratory correlations. Temperature, river discharge, sea level, and sunlight were examined. A multiplicative, environmental-dependent Ricker spawn–recruitment model was used to identify significant environmental variables. The model suggests a significant dome-shaped relationship between temperature and spawning success with an optimal temperature during larval stages resulting in maximum production of recruits. Also, increased spawning success is associated with increased summer river discharge. The significant environmental variables were included in the age-structured model in a stock–environment–recruitment relationship, and all model parameters were reestimated. The overall model fit improved only marginally with the inclusion of environmental variables, as indicated by the objective function value. However, the S–R component of the objective function dropped by 23% when environmental variables were included.

Les auteurs ont utilisé un modèle structuré en fonction de l'âge pour évaluer le recrutement de la population de hareng du Pacifique peuplant le détroit de Géorgie. Ce modèle est une version de celui décrit par Fournier et Archibald (1982. Can. J. Fish. Aquat. Sci. 39 : 1175–1207), modifié afin d'inclure les données de l'étude sur le frai. À cet effet, nous élaborons les trois hypothèses structurales suivantes : (1) la forme de la relation entre le frai réel et le frai observé, (2) la forme de la relation entre la remonte et le frai réel et (3) l'existence d'une relation frai–recrutement de type Ricker, avec une composante environnementale multiplicative. Afin de déterminer quels facteurs environnementaux ont eu une incidence significative sur le recrutement, nous avons tenté d'expliquer la variation résiduelle de la courbe de Ricker en termes des variables environnementales, à l'aide de corrélations préliminaires. La température, la débit fluvial, le niveau de la mer et la lumière solaire ont été étudiés. Pour identifier les variables environnementales significatives, nous avons utilisé un modèle multiplicatif de frai–recrutement de type Ricker tenant compte de l'environnement. Le modèle porte à croire qu'il existe une relation significative en dôme entre la température et le succès de la fraie ; une température optimale pendant les stades larvaires entraînes une production maximale des recrues. De plus, le succès accru de la fraie est associé à une augmentation du débit fluvial en été. Les variables environnementales significatives ont été incluses dans un modèle structuré en fonction de l'âge, dans une relation stock–environnement–recrutement, et tous les paramètres du modèle ont été réévalués. L'inclusion des variables environnementales n'a que marginalement amélioré l'ajustement du modèle global, comme l'indique la valeur de la fonction objective. Toutefois, la composante S–R de la fonction objective a baissé de 23 % à l'inclusion des variables environnementales.

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This study attempts to assess the role of environmental variation in the production of recruits of Pacific herring (*Clupea harengus pallasi*) in the Strait of Georgia. In the first part of this paper, we estimate recruitment for the Strait of Georgia herring population using age-structured model analysis. Next, we study the residuals from the estimated stock–recruitment relationship in light of environmental variation using the technique of "exploratory correlation" (Ricker 1975). We then develop an environmental-dependent Ricker spawn–recruitment regression model to determine significant environmental variables. This step is required because there is no formal way (in the statistical sense) to test significance of variables with the age-structured model. Finally, we combine significant environmental variables with the catch-at-age data for further stock reconstruction to examine overall model fit and parameter estimates.

A statistical approach to the stock and recruitment problem of commercially important pelagic species has only recently become possible because of the availability of long-term data on fish stocks and environmental conditions. Parrish and MacCall (1978) developed environmental-dependent recruitment functions for Pacific mackerel (*Scomber japonicus*). Multiple regression models utilizing environmental and density-dependent variables have also been developed to predict recruitment for Atlantic menhaden (*Brevoortia tyrannus*) (Nelson et al. 1976). The empirical approach, however, leaves the mechanisms controlling recruitment largely to speculation. It is generally agreed that the major factor affecting recruitment is larval survival. Generally, factors affecting larval survival are either density dependent (e.g. food, cannibalism) or density independent (e.g. ocean currents, temperature). Of course, prior knowledge of the magnitude of recruitment is very beneficial from a management standpoint.

Herring in British Columbian waters have supported commercial fisheries since 1877 (Hourston 1980). Although catch records date back to 1888, reliable records of the place, date, and quantity caught are available only since 1950. Landings have been sampled since 1933, and spawn surveys indexing escapement began in 1937. We limited our analysis to the period 1950–80. During this period the Strait of Georgia herring population has fluctuated considerably and has been subjected to heavy fishing pressure; also, the environment has shown considerable variation.

This study is based on an analysis of catch-at-age data. The model used is a modification of the age-structured model described in Fournier and Archibald (1982). The model includes subjective assumptions about the form of both measurement and process errors. A maximum likelihood method is used to simultaneously estimate all model parameters. These include natural and fishing mortality rates and stock–recruitment parameters. The ability of the model to incorporate additional information about populations was used to include the spawn survey data available for British Columbia herring, and environmental factors affecting recruitment.

Age-Structured Model Analysis

The basic inputs to the model are proportion-at-age caught in each season, total catch, and a spawn index. The model uses this information to reconstruct the population history for the Strait of Georgia herring population. Estimates are obtained for number of fish at age in the population each season, mortality rates at age each season, and stock–recruitment parameters. A maximum likelihood method is employed to simultaneously estimate all model parameters.

Model Description

The basic model has been described by Fournier and Archibald (1982) and only a cursory description is given here. We will describe in greater detail the new components added to incorporate spawn data. Three structural assumptions are made to include the spawn data: (1) the form of the relationship between the actual spawn and the observed spawn, (2) the form of the relationship between escapement and actual spawn, and (3) the existence of a Ricker spawn–recruitment relationship, with multiplicative environmental factors.

The data input for the age-structured component are estimates of the proportion of fish at age j in season i (S_{ij}) and estimates of the total number caught in season i (O_i). The statistical assumptions are (1) the estimated total catches have a log-normal error and (2) age structure estimates are obtained from a random sample of 400 fish taken from the catch each season and have a multinomial distribution. Thus, the log-likelihood equation for the actual percentage of fish of age j in the catch in season i (P_{ij}) and the actual number caught in season i (C_i), using natural logarithms, is

$$(1) \quad \sum_{i,j} S_{ij} \log P_{ij} - \sum_i \frac{1}{2}\left(\frac{\log O_i - \log C_i}{\sigma}\right)^2 - n \log \sigma$$

where σ^2 is the variance of the random variable $\log (O_i)$ and n is the number of seasons of fishing information.

Instantaneous fishing (F_{ij}) and natural (M_i) mortality rates are incorporated into the model through the catch equations (Ricker 1975):

$$(2) \quad P_{ij} C_i = [F_{ij}/(F_{ij} + M_i)][1 - \exp(-F_{ij} - M_i)]N_{ij}$$

where N_{ij} = number of age j fish in season i, F_{ij} = instantaneous fishing mortality of age j fish in season i, and M_i = instantaneous natural mortality of fish in season i. The F_{ij} were reparameterized in the VB form described in Fournier and Archibald (1982). We assumed that M_i is a density-dependent function of biomass B_i in season i. Given annual estimates of biomass:

$$(3) \quad B_i = \sum_j b_j N_{ij}$$

where b_j is average fish weight at age j we have

$$(4) \quad \log (M_{ij}) = m_0 + m_1(B_i - \bar{B})/\bar{B}$$

where $\bar{B}$ is average biomass and m_0 and m_1 are parameters to be estimated by the model. This parameterization of natural mortality is discussed in Fournier (1983).

Length times intensity of spawnings is used as an index of egg deposition. The index is related to the reproductive potential of the estimated escapement from the age-structured component of the model. We assume log-normal errors in the spawn data as well as in the estimates of reproductive potential. Incorporating the spawn index entails (1) defining the form of the actual spawn to true spawn relationship, (2) defining the form of the escapement to actual spawn relationship, and (3) assuming that a Ricker spawn–recruitment relationship with log-normal error exists.

We assume that the spawn measurements have been consistent within certain time periods (k). The time periods used (1951–68 (k = 1), 1969–75 (k = 2), and 1976–80 (k = 3)) were chosen because of apparent changes in the method of

recording spawn observations. Thus, the equation relating actual spawn (AS_i) to observed spawn (OS_i) in year i is given by

$$(5) \quad AS_i = OS_i CSP_k \exp(\epsilon_i)$$

where the ϵ_i are normally distributed random variables with mean 0 and variance σ_1^2 and CSP_k are actual spawn-observed spawn coefficients estimated for time period k given that $CSP_1 = 1$. The contribution to the objective function is

$$(6) \quad -\sum_i (\tfrac{1}{2}\sigma_1^2)[\log(AS_i/OS_i) - \log CSP_k]^2.$$

The actual spawn–escapement relationship is given by

$$(7) \quad AS_i = P_i \, QSP \exp(\epsilon_i)$$

where P_i = reproductive potential of population in season i, QSP = actual spawn–escapement coefficient, and ϵ_i = normally distributed random variables with mean 0 and variance σ_2^2.

The reproductive potential is defined as

$$(8) \quad P_i = \sum_j f_j N_{i+1,j}$$

where f_j = relative fecundity of age j fish.

The contribution of the actual spawn–escapement relationship to the objective function is

$$(9) \quad -\sum_i (\tfrac{1}{2}\sigma_2^2)[\log(AS_i/P_i) - \log QSP]^2.$$

The relationship relating spawn to the age-structured component of the model is a Ricker spawn–recruitment function defining recruitment as

$$(10) \quad N_{i+1,1} = \alpha \, AS_i \exp(-\beta \, AS_i + \epsilon_i)$$

where the ϵ_i are normally distributed random variables with mean 0 and variance σ_3^2 and α and β are spawn–recruitment parameters estimated by the model. The contribution to the objective function from this relationship is

$$(11) \quad -\sum_i (\tfrac{1}{2}\sigma_3^2)[\log(N_{i+1,1}/AS_i) - \log \alpha + \beta \, AS_i]^2.$$

The simultaneous estimation of all model parameters is done by a computer routine that minimizes the negative value of the log-likelihood function, or objective function. Thus, parameter estimates that reproduce the input data as closely as possible for a given set of assumptions are uniquely determined. Estimates of the variance of the three spawn relationships, σ_1^2, σ_2^2, and σ_3^2 are not estimated by the model, but are held at fixed values. These values are incorporated into the model as penalty weights, $w = 1/\sigma^2$. Penalty weights are assigned by the user to reflect his intuition about the relative accuracy of the data. The spawn-related penalty weights used in this analysis are 20 for the actual spawn–escapement relationship, 10 for the actual spawn–observed spawn relationship, and 5 for the actual spawn–recruitment relationship.

These penalty weights reflect our belief that herring do not follow a stock–recruitment relationship very strongly, and they express our uncertainty about the spawn index. By placing the highest weight on the actual spawn–escapement relationship, the actual spawn estimates will be forced to closely follow the escapement estimates from the age structure component (Stocker et al. 1983).

Estimates of Recruitment

Parameter estimates and the objective function value are given in Table 1. Density-dependent natural mortality rate follows an inverse relationship. That is, higher natural mortality rates are estimated for lower biomass. The objective function value for the model fit without environmental variables is 365.

TABLE 1. Model parameter estimates and objective function values for the Strait of Georgia herring population.

Parameter/function	Estimated value: Without environment	Estimated value: With environment
Instantaneous natural mortality rate	0.31–0.71	0.30–0.73
Actual spawn–escapement coefficient (QSP)	0.44	0.45
Spawn index conversion factor (CSP_k)		
$k = 2$ (1969–75)	1.17	1.18
$k = 3$ (1976–80)	1.32	1.27
Objective function value	365	364
S–R component of objective function	9.0	6.9

For the Strait of Georgia, mortality rates vary from 0.31 to 0.71, representing an annual survival rate ranging from 0.49 to 0.73. Estimates of the spawn index conversion factors for 1969–75 and 1976–80 are 1.17 and 1.32, respectively. This indicates that recent spawn measurements somewhat underestimate spawn depositions in the Strait of Georgia compared with earlier years.

Herring data are collected by season starting July 1 and ending June 30. We have adopted the convention of naming the cohort by season as fish in their first year of life. For example, spawn for the 1950–51 season (season i) is deposited in March of 1951 and produces the 1951 cohort of the 1951–52 season (season $i + 1$). The estimated recruitment, measured as $N_{i+1,1} \times 10^{-7}$, is shown in Fig. 1. Recruitment is highly variable showing a fourfold difference between the peak in 1964 and the trough in 1976. Generally, several seasons of weak recruitments follow a season of strong recruitment.

The log-normal residuals for the stock–recruitment relationship are shown in Fig. 2. The time sequence plot (Fig. 2a) indicates that if a long-term time effect existed in the spawn index, it has been accounted for by the actual spawn-observed spawn coefficient estimated by the model. This conclusion is based on the observation that the residuals seem to appear as a horizontal "band" (Draper and Smith 1966). Residuals plotted against estimated recruitments (Fig. 2b) show a systematic departure from the model. Negative residuals correspond to low recruitments, whereas positive residuals correspond to high recruitments. This phenomenon is generally observed in stock–recruitment analysis. The following section examines the presented residuals in light of environmental variation.

Residuals and Environmental Factors

To select significant environmental factors for inclusion in an environmental-dependent Ricker stock–recruitment model, we used the technique of "exploratory correlation" (Ricker 1975; Hayman and Tyler 1980). We correlated the residuals from the stock–recruitment relationship estimated by the age-structured model with monthly mean values of environmental factors thought important in the early life history of Pacific herring.

Generally, the major spawning season for herring in the Strait of Georgia is in March. Eggs are deposited on vegetation in and

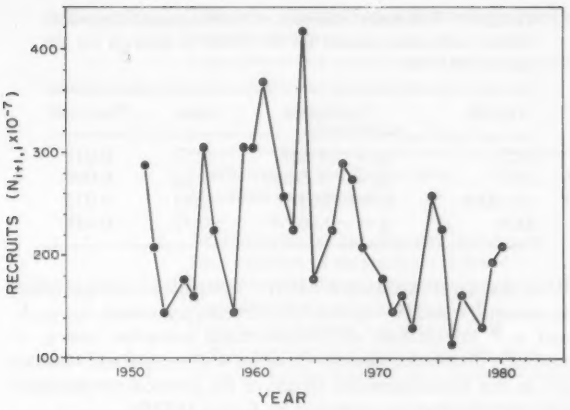

FIG. 1. Recruitment ($N_{i+1,1} \times 10^{-7}$) estimates from age-structured model analysis for the period 1951–80.

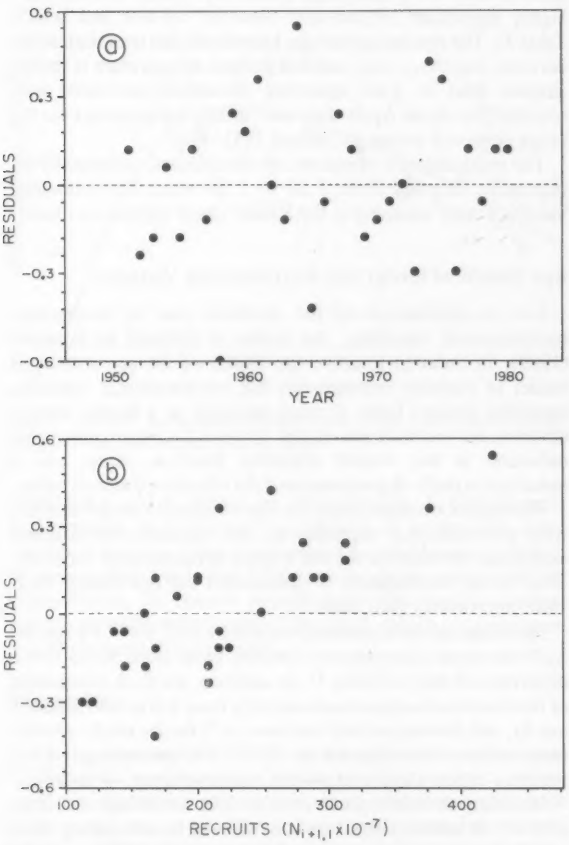

FIG. 2. Log-normal residuals of stock–recruitment relationship estimated from age-structured model analysis (a) versus time and (b) versus estimated recruitment.

immediately below the intertidal zone. During the first days after hatching (14–20 d after egg deposition), herring larvae are at the mercy of water currents. Currents may transport larvae to places where food supply may not be adequate. This occurs in years where runoff is greater than average and wind-driven

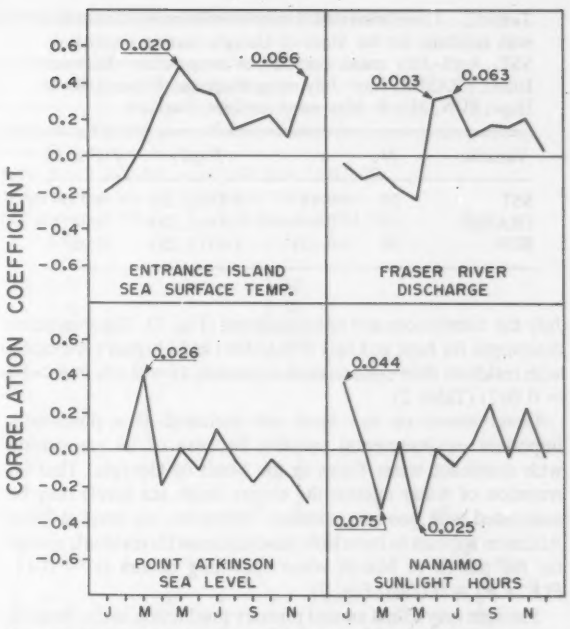

FIG. 3. Correlations between residuals from stock–recruitment relationships and monthly environmental variables for the Strait of Georgia herring population. Significant months are indicated with $P(F > \hat{F})$.

transport offshore has a net southward direction. During the summer the juveniles gather in large schools near the spawning grounds, and by the fall, schools gradually move to offshore wintering grounds (Hourston and Haegele 1980).

Environmental factors analysed in this study include monthly means of sea surface temperature, river discharge, sea level, and sunlight hours.

Sea surface temperature may influence recruitment through affecting egg and larval development, and food production. Generally, a dome-shaped relationship is expected between sea surface temperature and recruitment (Ricker 1975, p. 276). This would indicate that an intermediate temperature is most favorable, with less favorable temperatures above and below. We therefore looked for quadratic relationships between mean monthly sea surface temperature and residuals.

The correlation between temperature and residuals was generally positive (Fig. 3). Significant quadratic relationships occurred in May and December ($r = 0.50$ and 0.43 and $P(F > \hat{F}) = 0.020$ and 0.066, respectively). Analysis for the combined months during the period of larval development, April–July, showed a significant dome-shaped relationship between temperature (SST) and residuals (Table 2).

Fraser River discharge directly affects waters in the Strait of Georgia. Fresh water runoff creates a highly stable low-salinity surface layer (upper mixed layer). If the critical depth (Sverdrup 1953) is greater than the depth of mixing, a net increase in production can occur (Parsons 1965). In the Strait of Georgia, conditions to permit an increase in primary production occur during the period April–September. This production could benefit larval and juvenile herring on their respective feeding grounds.

River discharge shows a negative correlation with residuals from January through May, followed by a positive correlation from June through December. With the exception of June and

TABLE 2. Correlation coefficients of environmental variables with residuals for the Strait of Georgia herring population. SST, April–July mean sea surface temperature, Entrance Island; FRASER, June–July mean discharge, Fraser River at Hope; SUN, March–May mean sunlight, Nanaimo.

Variable	N	r	$\hat{F}$ (df)	$P(F > \hat{F})$
SST	30	0.417	2.85 (2, 29)	0.075
FRASER	30	0.366	4.33 (1, 28)	0.047
SUN	30	−0.351	3.93 (1, 28)	0.057

July the correlations are not significant (Fig. 3). The combined discharges for June and July (FRASER) had a higher correlation with residuals than either month separately ($r = 0.37$, $P(F > \hat{F}) = 0.047$) (Table 2).

Observations on sea level are included as a potentially important environmental variable because of its association with dominant water flows in the Strait of Georgia. That is, retention of water against the shores (high sea level) may be associated with good recruitment. However, sea level at Point Atkinson appears to have little association with residuals except for the month of March when spawning occurs ($r = 0.41$, $P(F > \hat{F}) = 0.026$) (Fig. 3).

Sunlight may affect annual primary production in the Strait of Georgia (Parsons et al. 1970). The correlations between monthly mean sunlight hours and residuals (Fig. 3) were significant for January, March, and May. The significant negative correlations for the spring are consistent with the descending portion of the dome-shaped relationship between temperature and residuals. That is, in years of high sunshine during spring and, hence, warmer temperatures, recruitment is considerably below average. The year 1958 is a good example when high sunlight hours in May produced one of the lowest recruitments in the Strait of Georgia (Fig. 1). Analysis for the combined spring months (SUN) showed a significant negative relationship between sunlight hours and residuals ($r = -0.35$, $P(F > \hat{F}) = 0.057$) (Table 2).

Environmental-Dependent Ricker Stock–Recruitment Models

The key environmental variables (Table 2) identified through exploratory correlations are included in an environmental-dependent multiple regression Ricker model. It is noteworthy that the environmental conditions that are correlated with recruitment have strong biological implications determining spawning success and egg, larval, and juvenile survival.

Multiple Regression Ricker Model

We used a multiple regression procedure to identify statistically significant environmental variables. The Ricker model was transformed to a linear function by taking natural logarithms:

$$(12)\quad \log(N_{i+1,1}/S_i) = \log\alpha - \beta S_i + \gamma_1 \mathrm{SST}_i + \gamma_2 \mathrm{SST}_i^2 + \delta \mathrm{FRASER}_i + \eta \mathrm{SUN}_i + \epsilon_i$$

where $N_{i+1,1}$ = estimated recruits (Fig. 1) in season i, S_i = spawn index in season i, SST_i = normalized sea surface temperature in season i, SST_i^2 = normalized square of sea surface temperature in season i, FRASER_i = normalized Fraser River discharge in season i, SUN_i = normalized sunlight hours in season i, α and β = spawn recruitment parameters, γ_1, γ_2, δ, and η = coefficients of environmental variables, and ϵ_i = normally distributed random variables with mean 0 and variance σ^2. In this formulation the effects of the physical environment are multiplicative as suggested by Ricker (1975).

TABLE 3. Parameter estimates of environmental-dependent Ricker recruitment model for the Strait of Georgia for the period 1951–80.

Variable	Coefficient	t-ratio	P(two-tail)
SST	$\gamma_1 = 0.33658$	2.77	0.011
SST^2	$\gamma_2 = -0.24639$	−3.22	0.004
FRASER	$\delta = 0.00016$	2.43	0.023
SUN	$\eta = -0.00198$	−0.77	0.451

The significant environmental variables are April–July mean sea surface temperature, square of temperature, and June–July mean Fraser River discharge (Table 3). These variables are highly significant (P(two-tail) between <0.001 and 0.023; Table 3). The results support the hypothesis that the relationship between log $(N_{i+1,1}/S_i)$ and sea surface temperature is dome-shaped. That is, good spawning success is associated with intermediate mean April–July sea surface temperatures for the range observed during the period 1951–80.

The residual sums of squares or unexplained variation of the regression dropped from 3.08 to 1.84 when environmental variables were included in the Ricker linear regression model.

Age-Structured Model with Environmental Variables

For an explanation of the methods used to incorporate environmental variables, the reader is referred to Fournier (1983). In order to improve the ability of the age-structured model to estimate recruitment, the environmental variables identified above (Table 3) were included in a Ricker stock–environment–recruitment model. Criteria for improvement is a reduction in the overall objective function value, and a reduction in the S–R component of the objective function value.

The results obtained from the age-structured model analysis with environmental variables are not qualitatively different from those obtained for the run without environmental variables. That is, the reestimation of parameters did not change their value appreciably (see Table 1).

Including the environmental variables (SST, SST^2, FRASER, SUN) decreased the objective function value from 365 to 364, a difference of only 1 (Table 1). In addition, the S–R component of the function decreased substantially from 9.0 to 6.9 (Tables 1 and 4), and the uncorrected variance (σ_3^2) for the stock–recruitment relationship dropped by 22%. The percentage of the variance of recruitment explained increased from 45 to 58%.

Including environmental variables does not change the shape of the S–R relationship. This is evidenced by comparing the α and β parameter estimates, and the level at which maximum reproduction occurs, for the two runs (see Table 4). The Ricker environmental-dependent S–R relationship estimated by the age-structured model is shown in Fig. 4. The level of spawn that would produce maximum recruitment on average is at 477. An interesting observation is that variability in recruitment appears to be much less at higher spawn levels.

The time sequence plots of residuals for the stock–recruitment relationship (open circles) and stock–environment–recruitment

TABLE 4. Comparison of information related to Ricker S–R relationship, without and with environmental variables.

Information	Ricker S–R relationship	
	Without environment	With environment
Coefficients for the Ricker curve	$\alpha = 1.44, \beta = 2.04$ E-03	$\alpha = 1.47, \beta = 2.09$ E-03
Maximum reproduction	0.62 times the average actual spawn of 785.1	0.61 times the average actual spawn of 781.3
Total variation for the estimated recruitment	3.28	3.34
Total variation of the residuals of the stock–recruitment relationship	1.81	1.39
Proportion of the variation explained	0.45	0.58
Uncorrected variance estimate for S–R	0.58 E-01	0.45 E-01
S–R component of objective function value	9.0	6.9

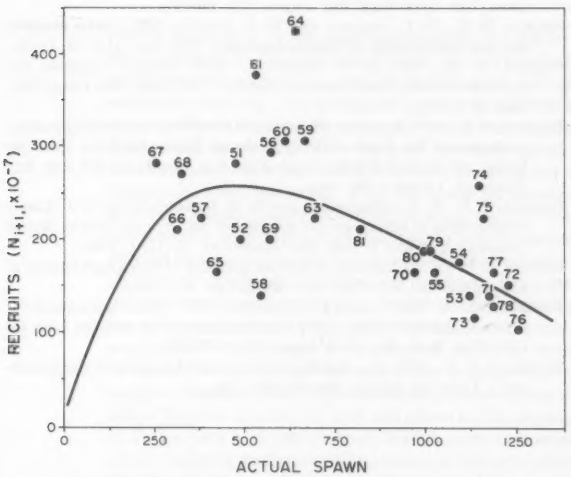

FIG. 4. Ricker environmental-dependent stock–recruitment model fitted to Strait of Georgia herring data.

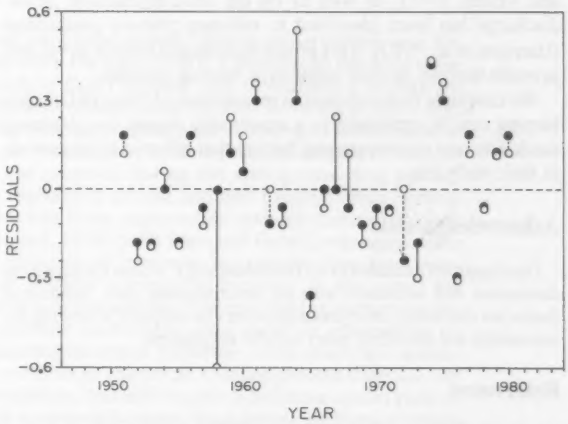

FIG. 5. Residual time sequence plots for Ricker stock–recruitment model (○) and Ricker stock–environment–recruitment (●) model.

relationship (solid circles) are shown in Fig. 5. Considerable improvement in predicting recruitment is evident for some individual seasons when environmental variables are included. It is interesting to note that 1958 gave the single most significant improvement. As already pointed out, 1958 was the warmest year on record for the period considered, which also produced one of the lowest recruitments.

Discussion

An age-structured model was used to estimate recruitment for the Strait of Georgia herring population. This model combines available biological information in a systematic way with catch-at-age data to produce a comprehensive analysis of past behavior of the exploited Strait of Georgia herring population. The model has the correct stochastic orientation, meaning that both the data submitted to the model and the underlying processes are subject to error, and that these errors are allocated in a reasonable fashion. Another advantage of this model is its ability of simultaneous estimation. That is, all data and all structural assumptions are included simultaneously in a single estimation procedure.

An important consideration in the detection of environmental factors affecting recruitment is the ability of the age-structured model to estimate the residuals of the stock–recruitment relationship correctly (Fournier and Archibald 1982). Results from their simulation study on a hypothetical fish population indicate that the model performed well in estimating residuals.

The biological assumptions made for this analysis included (1) time-dependent spawn index with the spawn index conversion factor evaluated for blocks of years, (2) density-dependent natural mortality, and (3) Ricker form of stock–recruitment. The first assumption expresses our belief that the completeness and quality of spawn surveys has improved over the years.

We found natural mortality to be inversely related to biomass, or depensatory. The principal mechanism suggested for depensation is increased natural mortality due to predation associated with smaller school sizes at low biomass (Clark 1974).

The Ricker model has a large compensatory density-dependent term which implies that at high biomass, recruitment is low. The mechanisms suggested for compensation in herring may be limited spawning substrate or cannibalism by second-wave spawners on first-wave spawned eggs. From our results (Fig. 4) we conclude that a functional density-dependent trend exists for Strait of Georgia herring. The degree of density dependence at the mean level of spawn ($-b\bar{S}$) was estimated at 1.43 based on average observed spawn (Cushing and Harris 1973), indicating moderate density dependence. They found the average density dependence for four Pacific herring stocks to be

1.16. The implications of moderate density dependence are that Pacific herring (1) lack strong regulatory mechanisms for stabilizing population size, (2) show high natural fluctuations in recruitment, and (3) are quite susceptible to over exploitation.

We used an empirical approach to incorporate environmental effects into stock–recruitment models. Through this approach we have identified environmental factors that are important, along with spawning stock size, in determining recruitment for the Strait of Georgia herring population. This knowledge can be of great importance in identifying years of poor recruitment well before the year-class enters the fishable stock.

Environmental factors identified to be significantly related to estimates of recruitment of Strait of Georgia herring were sea surface temperature and Fraser River discharge. Temperature has been identified as important, as it has a direct physiological effect on the development of herring eggs and larvae (Alderdice and Velsen 1971), as well as on the food production. River discharge has been identified to enhance primary production (Harrison et al. 1983). This production should benefit larval and juvenile herring on their respective feeding grounds.

We conclude that variation in recruitment of Strait of Georgia herring can be explained to a reasonable degree by spawning stock size and environmental factors that effect critical periods in their early life.

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Productivity of Pacific Herring (*Clupea harengus pallasi*) in the Eastern Bering Sea under Various Patterns of Exploitation[1]

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Pacific herring (*Clupea harengus pallasi*) is a major food source for western Alaska native people and has been commercially exploited in the eastern Bering Sea since the early 1900's. Commercial harvests were small and localized in coastal waters until foreign factory fleets located and developed a fishery on wintering herring concentrations in the early 1960's. Harvests peaked near 150 000 t in the early 1970's and then declined along with catch per unit effort. Foreign harvests were eliminated following establishment of the United States 200 mile Fishery Conservation Zone. In recent years a fishery has developed in State of Alaska coastal waters which harvests herring for sac roe (ovaries) during the spring spawning period. Proposals have been put forth by trawl fishermen to reestablish a food and bait fishery within Federal waters. Development of offshore mixed stock fisheries has been opposed by inshore commercial and subsistence users who fear that stocks will be overexploited. While both State and Federal managers have agreed to give subsistence users and inshore domestic commercial fishermen top priority, they have been unable to agree upon plans for dealing with potential offshore commercial harvests. In this paper we present results of a computer model that we developed to examine effects of various fishing patterns upon herring productivity and yield. Within our model, maximum sustainable yield (MSY) is achieved at an exploitation rate (E) of 0.3 (i.e. harvest of 30% of total spawning biomass). However, since stocks still appear to be below MSY biomass and since productivity and yield drop sharply at E values greater than 0.3, we suggest that an E of 0.2 be maintained under current conditions. This will result in a potential loss in yield of only 7% from an E of 0.3, but will allow a 52% increase in spawning biomass. Four fishing patterns in which both discrete and mixed stock fishery removals were allowed to occur were also examined. During years in which inshore fisheries fail to harvest 20% of available spawning biomass, an offshore allocation of up to 10 000 t could be permitted with minimal risk to damaging the reproductive potential of small spawning stocks. However, results indicated that mixed stock fisheries should be restricted to lower levels than would be appropriate for fisheries targeting on discrete stocks to avoid risks of overharvesting some stocks.

Le hareng du Pacifique (*Clupea harengus pallasi*), qui représente une importante source de nourriture pour les autochtones de l'Alaska occidental, fait l'objet d'une pêche commerciale dans l'est de la mer de Béring depuis le début du siècle. Jusqu'à ce que les flottilles étrangères de bateaux-usines découvrent et exploitent, au début des années 1960, une pêcherie où se regroupait les harengs en hiver, les captures commerciales étaient faibles et se resteignaient aux eaux côtières. Au début des années 1970, les prises ont atteint presque 150 000 t pour ensuite péricliter, tout comme la prise par unité d'effort. L'établissement de la zone de conservation des pêches jusqu'à 200 milles des côtes américaines a éliminé l'exploitation étrangère. Récemment, on a vu se développer dans les eaux côtières de l'Alaska une pêche axée sur l'exploitation de la rogue (ovaires) du hareng au cours de la fraie printanière. Les pêcheurs au chalut ont présenté des propositions visant le rétablissement d'une pêche du hareng comme aliment et comme appât, dans les eaux relevant de la compétence fédérale. Les pêcheurs commerciaux et autochtones côtiers, qui craignent la surexploitation des stocks, s'opposent au développement de pêches hauturières de stocks mixtes. Quoique les gestionnaires du palier fédéral et de l'État de l'Alaska ont consenti à donner la priorité aux pêcheurs autochtones et aux pêcheurs commerciaux côtiers de l'endroit, ils n'ont pu s'entendre sur des plans d'exploitation commercial hauturière. Le présent rapport porte sur les résultats d'un modèle informatisé que les auteurs ont élaboré en vue d'étudier l'incidence de différents schèmes de pêche sur la productivité et le rendement du hareng. Dans ce modèle, le rendement maximal soutenu (RMS) est atteint à un taux d'exploitation (E) de 0,3 (c.-à-d. la pêche de 30 % de la biomasse totale de géniteurs). Toutefois, on croit que E devrait être maintenu à 0,2 dans les conditions actuelles, étant donné que les stocks semblent encore être inférieurs à la biomasse au RMS et que la productivité et le rendement chutent quand la valeur de E dépasse 0,3. Cela ne représenterait qu'une baisse potentielle du rendement de l'ordre de 7 % par rapport à une valeur de $E = 0,3$, mais permettrait une augmentation de 52 % de la biomasse de géniteurs.

[1]This paper was presented at the International Symposium on the Biological Characteristics of Herring and Their Implication for Management, convened at Nanaimo, B.C., June 20–22, 1983, commemorating the 75th anniversary of the Pacific Biological Station.

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On a aussi examiné quatre schèmes de pêche où des captures dans les stocks isolés et mixtes étaient effectuées. Au cours des années où les pêches côtières n'exploitent pas 20 % de la biomasse disponible de géniteurs, on pourrait allouer un contingent hauturier totalisent jusqu'à 10 000 t sans risque majeur pour le potentiel reproducteur de petites fraies. Toutefois, les résultats portent à croire qu'une pêche visant les stocks mixtes devrait être restreinte à des niveaux inférieurs à ceux appropriés pour une pêche axée sur des stocks isolés afin qu'il n'y ait pas surexploitation de certains stocks.

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Although Pacific herring, *Clupea harengus pallasi*, have been harvested for food by people living in eastern Bering Sea coastal villages since at least 500 B.C. (Hemming et al. 1978), development of large-scale commercial fisheries did not begin until the twentieth century. The first commercial fisheries occurred in Norton Sound (1909) and off Unalaska Island (1928) (Rounsefell 1929). Annual harvests were low (3–2700 t), and these fisheries ended in the late 1940's (Wespestad and Barton 1981). Beginning in 1959, Soviet trawl vessels, joined in later years by Japanese trawl and gillnet vessels, began to harvest large quantities of herring in eastern Bering Sea offshore waters. Annual harvests reached a peak of 146 000 t in 1970 and then declined along with catch per unit of effort. Offshore herring fishing was eliminated in 1980 when herring was made a prohibited species within the Fishery Conservation Zone. As foreign offshore herring harvests declined, inshore domestic harvests rose from an annual mean of less than 100 t during 1967–76 to 17 000 t during 1977–83. Most of the domestic harvest has been taken for sac roe (ovaries) (30 750 t in 1983) during the spring spawning period; some has been taken for other food uses and bait (3243 t in 1982) during the summer. A herring spawn on kelp harvest (rockweed kelp, *Fucus* sp.) has also developed along with sac roe fisheries (148 t in 1983). Total value of these harvests to United States fishermen has risen from less than $1 million in 1977 to $13 million in 1983.

Due to the limited information available on population biology of eastern Bering Sea herring, and in view of stock collapses that have commonly plagued herring fisheries in other parts of the world (see e.g. Cushing 1981; Blaxter and Hunter 1982, and references therein), much controversy surrounds management practices. Inshore fisheries, regulated by the State of Alaska, have been limited to a maximum exploitation rate of 20% of available spawning biomass for sac roe harvests, while quotas have been established for summer food and bait harvests (3200 t) and spring spawn on kelp harvests (10% of available kelp standing crop). Offshore herring fisheries, pending development of a management plan by the North Pacific Fisheries Management Council, have been prohibited, although about 2000 t of herring are taken incidentally during groundfish trawl fisheries. Opponents of offshore fisheries contend that eastern Bering Sea herring stocks are already fully utilized by inshore commercial and subsistence users and that offshore fisheries present the added risk of fishing upon unknown mixtures of spawning stocks. Proponents of offshore fisheries counter that assessment techniques and exploitation rates used for inshore fisheries are overly conservative (i.e. herring stocks are not being fully utilized) and that too much of the harvest is allocated to the sac roe fishery (i.e. markets for other herring products need to be developed).

Wespestad and Francis (1980) used a deterministic model, in which complete randomness was assumed for stock distribution and fishery removals, to examine effects of mixed stock harvests on eastern Bering Sea herring. They concluded that exploitation rates would be proportional to individual stock abundance. However, little data exist on the offshore distribution of herring, making it difficult to verify assumptions used in their analysis.

The purpose of this study was to determine effects of various exploitation rates on biomass and yield of eastern Bering Sea herring stocks and to examine consequences of mixed stock fisheries using a stochastic simulation model. Specific objectives were to determine whether the model's behavior was consistent with available information and to evaluate current and proposed management strategies within the context of these results. No attempt was made to simulate density-dependent or environmental effects upon growth and natural mortality rates or sexual maturity schedule within the model.

Model Parameters

Stock Composition and Distribution

Six spawning groups of herring have been recognized for management purposes by the State of Alaska: Togiak, Security Cove, Goodnews Bay, Nelson Island, Cape Romanzof, and Norton Sound (Fig. 1). Spawning stock affinities of herring on the winter grounds have not been determined, but are thought to be a mix of the above-cited stocks. Aerial survey assessments of these spawning groups during 1978–82 indicated that Togiak comprised the largest group of spawners each year, averaging 82% of total estimated spawning biomass (Fried et al. 1982a). Security Cove, Goodnews Bay, Nelson Sound, Cape Romanzof, and Norton Sound averaged 3, 2, 3, 2, and 8%, respectively. Although electrophoretic studies failed to demonstrate significant genetic differences among these spawning groups (Grant 1981), consistent differences in growth patterns among these groups have been found (Walker and Schnepf 1982; Barton and Steinhoff 1980; Rowell 1980; also see Age and Growth section below). Therefore, each of the six spawning groups was assumed to be a valid stock for the purposes of the present study. Other minor spawning groups occur along the Alaska Peninsula and Aleutian Islands (Warner and Shafford 1977; Wespestad and Barton 1981), but were excluded from consideration within the present study.

Age and Growth

Herring usually enter eastern Bering Sea commercial catches between the ages of 3 and 5 yr (Wespestad and Barton 1981; Fried et al. 1982b, 1982c). Herring older than 9 or 10 yr are uncommon in commercial and survey catches, although some may reach a maximum age of at least 15 yr. Within simulations herring were allowed to attain a maximum age of 10 yr.

Mean size at each age decreases for eastern Bering Sea herring spawning stocks located progressively northward from

FIG. 1. Eastern Bering Sea, Alaska, showing locations discussed in the text.

Togiak (Barton and Steinhoff 1980; Fried et al. 1982b, 1982c). However, comparisons of von Bertalanffy age–length growth curves for these six stocks, using the least squares technique of Kappenman (1981), revealed that two different curves described growth: one for the southern stocks (Togiak, Security Cove, and Goodnews Bay), $L_S = 314.44\{1 - \exp[-0.22(t + 2.23)]\}$, and another for the northern stocks (Nelson Island, Cape Romanzof, and Norton Sound), $L_N = 289.07\{1 - \exp[-0.29(t + 0.97)]\}$, where L_S and L_N are standard lengths (millimetres). Age-specific lengths computed from the two von Bertalanffy curves were converted to weights using a weight–length regression (Ricker 1975). A single weight–length equation was calculated for all spawning groups, since geographic trends were not evident: $W = 10^{-6}L^{3.479}$, where W and L are weight (grams) and standard length (millimetres), respectively. Seasonal changes in growth rate were not simulated in our model, since most commercial harvests under present and proposed management regimes would occur when herring were at or near maximum age-specific weights (i.e. spring sac roe and winter trawl harvest periods). Growth was increased uniformly in quarterly increments each year so that herring reached maximum age-specific weight in the spring of each year, prior to spawning (Fig. 2).

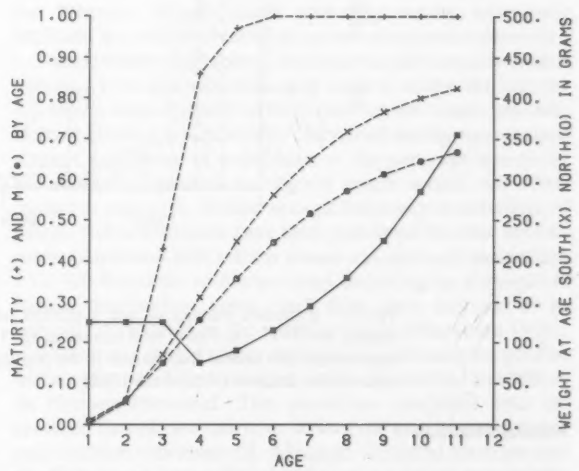

FIG. 2. Population parameters used in the model to simulate responses of eastern Bering Sea Pacific herring stocks to various patterns of exploitation. Maturity and instantaneous natural mortality schedules from Wespestad (1982).

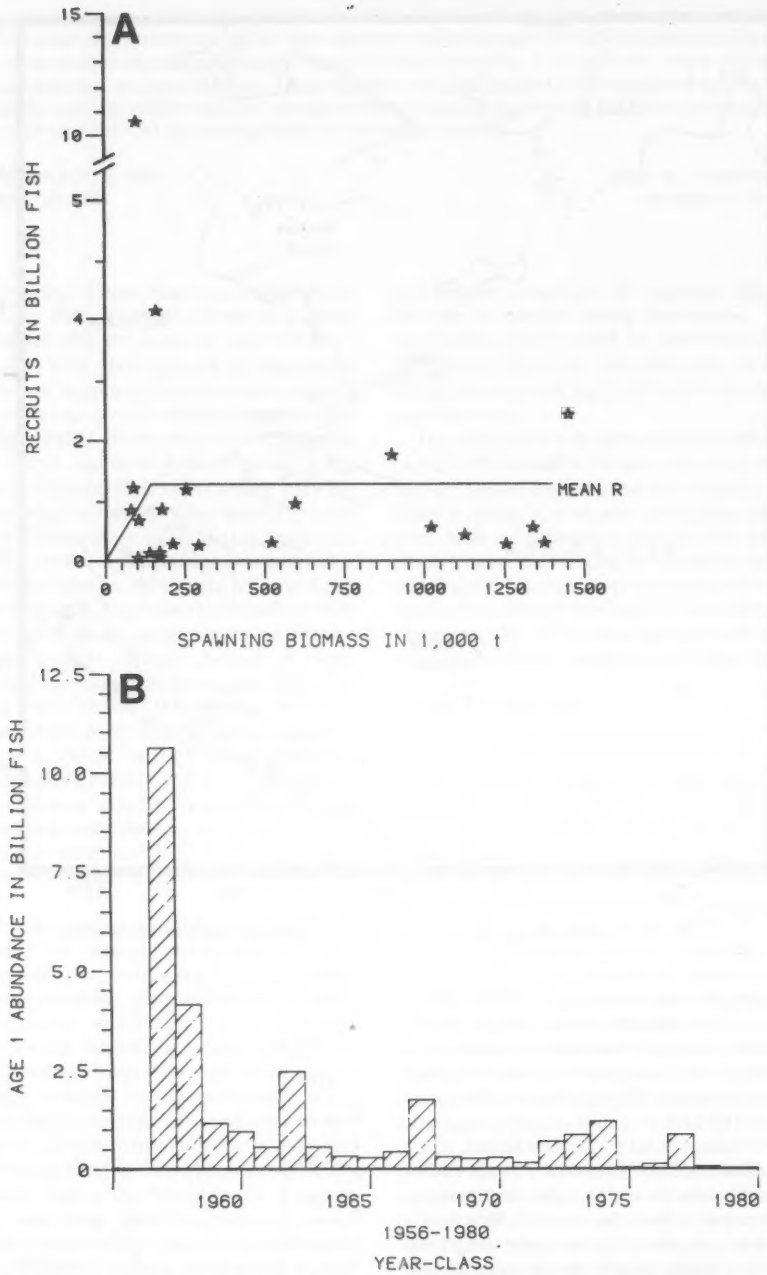

FIG. 3. Estimated number of age 1 recruits for all six eastern Bering Sea Pacific herring stocks, Alaska, 1957–77. (A) Plot of total number of age 1 recruits and the total spawning biomass of the parental populations; (B) annual fluctuations in the population size at age 1 of the 1957–77 year-classes. Data from cohort analysis (Wespestad 1982).

Natural Mortality

Little information on natural mortality rates is available for eastern Bering Sea herring. Wespestad (1982), using the Alverson and Carney (1975) procedure, estimated average instantaneous natural mortality (M) for Bering Sea herring to be 0.39, only slightly higher than the 0.36 value obtained for British Columbia herring by Schweigert and Hourston (1980). However, age-specific M values calculated from catch data (e.g. 0.15 for age 4 to 0.36 for age 9) (see Fig. 4) were lower than those available for either British Columbia (e.g. 0.43 for age 4 to 1.18 for age 9) (Tester 1955; Taylor 1964) or Gulf of

TABLE 1. Values used in a model to generate recruitment vectors for eastern Bering Sea Pacific herring spawning groups.

	Spawning group						
	Togiak	Security Cove	Goodnews Bay	Nelson Island	Cape Romanzof	Norton Sound	Total
Mean recruitment: billions of age 1 herring (biomass, t)	1.051 (65 264)	0.038 (2388)	0.026 (1592)	0.038 (2388)	0.026 (1592)	0.102 (6367)	1.281 (79 591)
Critical biomass (t)	118 982	4353	2902	4353	2902	11608	145 100
Correlation matrix: year-class association between spawning groups							
Togiak	1.0	0.9	0.9	0.9	0.8	0.8	
Security Cove		1.0	0.9	0.9	0.8	0.8	
Goodnews Bay			1.0	0.9	0.8	0.8	
Nelson Island				1.0	0.8	0.8	
Cape Romanzof					1.0	0.9	
Norton Sound						1.0	

Alaska (e.g. 0.20 for age 4 to 0.85 for age 9) (Skud 1963) herring. For most of our simulations, Wespestad's (1982) age-specific M values were used for all stocks (see Fig. 4). However, to test sensitivity of the model's behavior to changes in M, some simulations were done with a constant M of either 0.30 (slightly higher than the mean age-specific rate of 0.27) or 0.39 (the highest estimated M value for these stocks). Values of M were applied in quarterly increments each year using a standard population decay function (Ricker 1975).

Sexual Maturity

Sexual maturity of eastern Bering Sea herring coincides with recruitment into sac roe fisheries. Although some herring reach maturity by 2 yr of age, most do not mature until they are 3–5 yr old (N. I. Naumenko, Pac. Res. Inst. Fish. Oceanogr. (TINRO), Vladivostok, USSR, unpubl. data; Wespestad 1982). Data from 1959–77 offshore herring harvests indicate that recruitment into that fishery also coincided with sexual maturity, since few 1- and 2-yr-old herring were caught. The reported mean maturity schedule for 1959–77 was used to calculate spawning stock size within our model (Fig. 2).

Recruitment

The spawner–recruit relationship was derived from estimates of spawning biomass and numbers of 1-yr-old herring obtained by cohort analysis (Wespestad 1982) (Fig. 3A). A Ricker recruitment curve did not fit our data (ANOVA, $P > 0.05$), although such a relationship has been used to describe recruitment within British Columbia and Southeastern Alaska herring stocks (International North Pacific Fisheries Commission 1961). Lack of fit does not preclude the existence of such a relationship for Bering Sea herring stocks. However, the relationship may be masked by environmental factors, which have been shown to be important in determining year-class strength in other herring populations (Taylor 1964; Iles and Sinclair 1982; Skud 1982).

Since a Ricker recruitment curve did not fit our data, we incorporated a nonrandom, linear spawner–recruit relationship within our simulations at low levels of spawning biomass, and assumed that recruitment varied randomly about a mean value (1.28 million 1-yr-old herring) above a critical threshold spawning biomass of 145 100 t (10% of maximum estimated spawning biomass). Recruitment was generated for each of the six stocks within our model by apportioning threshold biomass and mean number of recruits according to the mean observed distribution of total spawning biomass (Table 1). We assumed that adjacent stocks would have a high level of correlation in recruitment within a given year and that stocks spawning at increasing distances from one another would have less similar levels of recruitment. A correlation matrix, used to simulate these interstock relationships, and the coefficient of variation of annual numbers of 1-yr-old recruits, calculated from cohort analysis estimates (1.78), were used to produce a covariance matrix for generating multivariate normal residuals (Naylor 1966). These residuals were added to the mean recruitment value to simulate recruitment for spawning biomass above the threshold. Negative recruitment values were converted to zero.

Fishery Simulation Characteristics

During sac roe and subsistence fishery simulations, catchability was assumed to be equal for all sexually mature herring. Harvests were taken prior to spawning, were considered to be instantaneous, and preceded natural mortality for the spring quarter. All stocks except Nelson Island were subjected to sac roe fisheries. Nelson Island spawning herring were only exploited at a rate equivalent to current subsistence removals.

During winter trawl fishery simulations, only sexually mature herring 4 yr of age and older were made available for harvest. All stocks were assumed to be present on the winter grounds. Herring biomass was randomly distributed among various sized schools, composed of individuals of the same age and stock, according to a gamma distribution (mean school size 100 t, minimum size 10 t). Similar skewed frequency distributions of pelagic fish school sizes have been postulated by other investigators (Anderson 1981). Each school was randomly assigned to 1 of 100 locations within an array according to a univariate normal distribution, since catch data show biomass to be normally distributed on the winter grounds (Wespestad 1978).

Fishing was started within the location containing the greatest herring biomass. One school was randomly selected and 20% of its biomass harvested. This procedure continued until the specified harvest was taken, or 90% of the total biomass within each location was removed. Although simulated catch per unit of effort (mean approximately 20 t per trawl haul) was higher than that achieved historically by Soviet and Japanese vessels (3.5–8.5 t per trawl haul) (Shaboneev 1965; fishery observer data, Northwest and Alaska Fishery Center, NMFS), we felt

TABLE 2. Eastern Bering Sea Pacific herring sac-roe yield and spawning biomass from computer simulations using different levels of constant and variable exploitation. Results of 20 replicated 100-y simulations for each level of E and E_{MSY}.

Sac roe exploitation rate (E)	Spawning biomass (t) remaining after sac roe harvest			Sac roe harvest (t)		
	Mean	SD	Range	Mean	SD	Range
Constant proportion of spawning biomass removed						
0.0	791 041	131 279	247 631 – 1 023 287	531[a]	83[a]	183 – 679[a]
0.1	547 264	82 960	221 272 – 705 141	59 010	8 898	23 910 – 76 122
0.2	377 870	51 767	180 854 – 471 237	88 915	12 205	43 071 – 115 814
0.3	248 812	29 280	143 969 – 321 450	95 716	11 253	55 679 – 124 009
0.4	127 832	22 980	83 071 – 179 749	68 818	14 209	41 365 – 98 066
0.5	41 740	22 902	17 969 – 130 151	22 171	22 114	1 919 – 121 033
0.6	24 571	14 713	15 620 – 106 656	9 720	21 789	503 – 145 204
Variable proportion of spawning biomass removed based on different E_{MSY} values						
0.2	324 817	25 862	209 475 – 374 350	96 792	17 966	28 995 – 140 673
0.3	194 791	9 417	155 910 – 216 837	102 319	15 783	46 077 – 140 425
0.4	84 809	4 209	64 440 – 95 025	51 749	15 828	28 995 – 187 603

[a]Nelson Island stock exploited at constant rate of 0.03 in all cases to simulate subsistence harvest.

these values were reasonable with presently available fishing gear and electronics.

Management Strategies

Management of Alaska roe fisheries is based on applying exploitation rates (E) of 0.10–0.20 on discrete stocks. However, the rationale for this range of E values has not been investigated quantitatively. We used our model to examine effects of E values ranging from 0.00 to 0.60 on total yield and spawning biomass of eastern Bering Sea herring. Each experiment consisted of 20 replicated 100-yr simulations at a constant level of E. For each experiment, E was incremented by 0.10 for each stock except Nelson Island. This stock was harvested at an E of only 0.03 during all experiments to simulate subsistence removals. To begin each simulation the total population was set equal to that estimated by cohort analysis for 1978 (Wespestad 1982): total biomass 255 000 t (1- to 3-yr-old herring 40% of total population); spawning population 171 000 t.

Federal draft plans for an offshore mixed stock herring fishery (North Pacific Fishery Management Council 1983) propose that harvests be based upon a variable E calculated annually by the following equation:

$$E_i = E_{MSY}(B_i/B_{MSY})$$

where E_{MSY} = exploitation rate that achieves maximum sustainable yield (MSY), B_{MSY} = spawning biomass that produces MSY, and B_i = estimated spawning biomass in year i. The proposed E_{MSY} is 0.20, the maximum E allowed by State guidelines; B_{MSY} is 244 000 t, which is based upon past offshore harvest under an assumed E value of 0.20.

We examined effects of using a variable E on yield and spawning biomass in the same manner used for constant E: 20 replicated 100-yr simulations for each case investigated; initial population size and age structure set at the 1978 level. Three different cases were tested by substituting three pairs of E_{MSY} (0.20, 0.30, and 0.40) and B_{MSY} (obtained from simulations in which constant E values of 0.20, 0.30, and 0.40 were used) values into the above equation.

To investigate effects of offshore mixed stock harvests on inshore catches and spawning biomass, we assumed that all stocks were available to the winter trawl fishery and that the five smallest stocks (18% of total biomass) were always exploited at the presently accepted maximum rate of 0.20 for inshore fisheries. Surplus for harvest offshore was provided by decreasing inshore exploitation rate on the Togiak stock to either 0.00 or 0.15. This provides a potential offshore allocation equal either to 20 or 5% of the Togiak spawning biomass. Four patterns of fishing were examined by replicating 100-yr simulations 20 times for each pattern: (1) Togiak inshore E = 0.00, offshore harvest = maximum of 10 000 t; (2) Togiak inshore E = 0.15, offshore harvest = maximum of 10 000 t (maximum harvest currently proposed); (3) Togiak inshore E = 0.00, offshore harvest = 20% Togiak spawning biomass; (4) Togiak inshore E = 0.15, offshore harvest = 5% Togiak spawning biomass. To begin each simulation the total population was set equal to that estimated for 1959: total biomass 1 446 000 t (1- to 3-yr-old herring 89% of total population); spawning biomass 255 000 t.

Results and Discussion

Behavior of the Model

Without commercial removals, mean total spawning biomass for the model was 791 041 t (SD 131 279 t) (Table 2; Fig. 4A). Maximum yield was reached with a constant E of 0.30 where mean total spawning biomass was 248 812 t (SD 29 280 t) and mean total sac roe harvest was 95 716 t (SD 11 253 t). Both mean total spawning biomass and harvest declined sharply when E values exceeded 0.30. Similar results were obtained using a variable E calculated from specified values of E_{MSY} and B_{MSY}. Maximum yield occurred when E_{MSY} was set at 0.30. Although mean spawning biomass was less variable (F-test, $P < 0.05$), but lower (t-test, $P < 0.05$), when using variable E values, yield was not less variable (F-test, $P > 0.05$) or greater (t-test, $P > 0.05$) than when using constant E values. These results are not surprising, since the variable E procedure is based upon assumption of a Ricker spawner–recruit relationship. The spawner–recruit relationship within our model was not domed

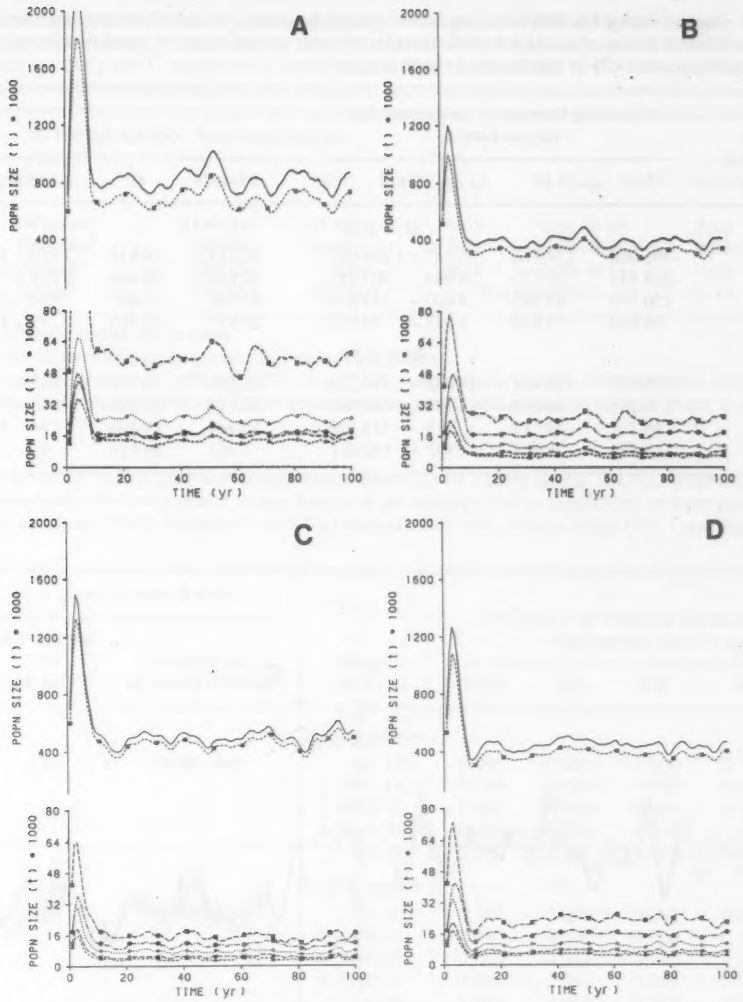

FIG. 4. Annual fluctuations in biomass in simulated eastern Bering Sea Pacific herring spawning populations subjected to various patterns of exploitation. (A) All stocks unexploited except Nelson Island ($E = 0.03$); (B) all stocks exploited at $E = 0.20$ except Nelson Island ($E = 0.03$); (C) exploitation pattern III in Table 5; (D) exploitation pattern IV in Table 5. Solid line = all stocks combined; asterisk = Togiak; cross = Security Cove; × = Goodnews Bay; circle = Nelson Island; triangle = Cape Romanzof; square = Norton Sound.

but generated random recruitment values about a specified mean over a wide range of spawning biomass values.

Simulations in which constant M values (greater than the mean of age-specific M values) were used achieved maximum yield with a constant E of 0.20 (Table 3). Mean yield at both constant M values tested was less than that achieved at similar E values when age-specific M values were used.

Model results conform to historical trends of spawning biomass and exploitation rates for the fishery (Table 4). Estimated mean total spawning biomass during a period of low exploitation (1960–66) was 1 166 000 t (SD 291 430 t). Although this is about 1.5 times greater than the mean spawning stock size, results from cohort analysis (Wespestad 1982) indicate that population structure was unusual during 1960–66 due to presence of the extremely abundant 1957 and 1958 year-classes. The 1957 year-class was 8 times greater than estimated mean annual recruitment of age 1 herring, (mean 1.3×10^9 individuals; 1957 year-class, 10.6×10^9). No other year-class has since approached this abundance (Fig. 3B).

During the most intensive period of offshore exploitation (1968–77) mean E was 0.33, but reached a maximum of 0.68 one year. Mean spawning biomass and harvest declined during this period as occurred during simulations with the model at E values greater than 0.30 (Tables 2 and 4). In more recent years (1978–82) E has been below 0.3, and often below 0.2. However, populations have probably not yet recovered from previous high exploitation rates. Estimated mean total spawning biomass during 1968–82 has been about 160 000 t.

TABLE 3. Eastern Bering Sea Pacific herring sac-roe yield and spawning biomass from computer simulations using two different values of constant natural mortality (M) and several levels of constant exploitation (E). Results of 20 replicated 100-yr simulations for each level of E.

Sac roe exploitation rate (E)	Spawning biomass (t) remaining after sac roe harvest			Sac roe harvest (t)		
	Mean	SD	Range	Mean	SD	Range
			M = 0.30			
0.1	391 090	174 288	50 237 – 1 254 038	42 113	18 838	5 319 – 135 221
0.2	265 337	128 778	28 944 – 907 412	62 169	30 496	6 518 – 214 163
0.3	150 330	95 385	4 860 – 539 818	56 768	37 607	854 – 211 320
0.4	53 810	52 835	1 028 – 34 076	25 877	31 305	82 – 198 140
			M = 0.39			
0.1	235 925	116 192	24 841 – 814 276	25 360	12 539	2 617 – 87 708
0.2	130 286	88 098	2 739 – 492 306	30 123	20 896	300 – 116 220
0.3	44 772	49 110	519 – 313 526	15 464	19 495	44 – 122 263
0.4	19 398	26 874	445 – 162 811	7 663	16 413	14 – 93 998

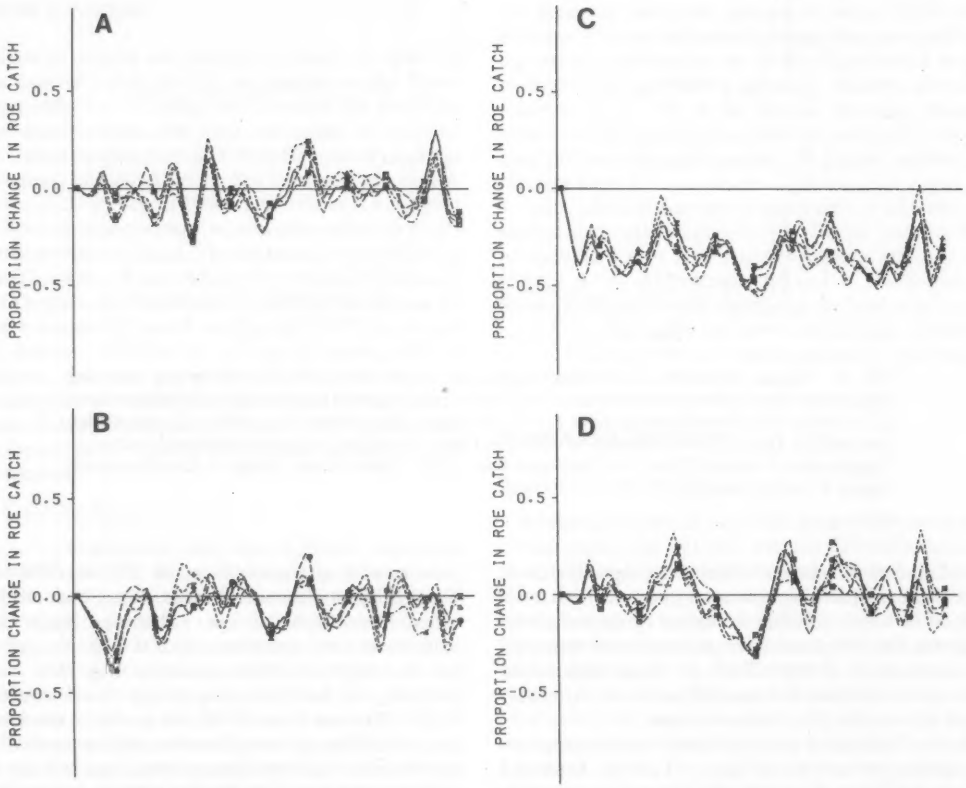

FIG. 5. Annual departures from expected mean yield (based upon $E = 0.03$ for Nelson Island and $E = 0.20$ for all other stocks) when different combinations of discrete and mixed stock fishery removal occur. (A) Exploitation pattern I in Table 5; (B) exploitation pattern II in Table 5; (C) exploitation pattern III in Table 5; (D) exploitation pattern IV in Table 5. Symbols as defined in Fig. 4.

TABLE 4. Eastern Bering Sea Pacific herring spawning biomass and commercial fishery exploitation rates during 1960–82. Spawning biomass estimates obtained from cohort analysis (Wespestad 1982) unless otherwise indicated. Total and spawning biomass exploitation rates (E_T and E, respectively) were calculated from catches listed by North Pacific Fishery Management Council (1983) unless otherwise indicated.

Period	Area of catch	Spawning biomass		E_T		E	
		Mean	SD	Mean	Range	Mean	Range
1960–66	Offshore[a]	1 166 000	291 430	0.01	0.01–0.03	0.02	0.01–0.04
1968–77	Offshore[b]	189 400	134 638	0.21	0.09–0.44	0.33	0.12–0.68
1978–81	Inshore[c]	166 750	7 228	0.11	0.09–0.13	0.15	0.12–0.18
1978–82[d]	Inshore	161 540	68 472	Not available		0.14	0.04–0.29

[a]Entire harvest offshore except 18 t in 1964.
[b]Less than 1% of total harvest inshore except 1977 when 12% inshore.
[c]Transition to total inshore harvest: 1978 and 1979, 31 and 38%, respectively, inshore; 1980–82 entire harvest inshore.
[d]Data from Alaska Department of Fish and Game aerial assessments and inshore sac roe harvests (Fried et al. 1982a).

TABLE 5. Probability of achieving various total annual exploitation rates (E_T) for eastern Bering Sea Pacific herring stocks subjected to four different fishing patterns simulated with the computer model. Results of 20 replicated 100-yr simulations for each pattern examined. Spawning stocks used in the model were Togiak (TOG), Security Cove (SC), Goodnews Bay (GB), Nelson Island (NI), Cape Romanzof (RO), and Norton Sound (NS).

Annual exploitation rate or quota for each fishery					Probability of obtaining various ranges of total annual exploitation rates for spawning stock					
Sac roe (E)		Subsistence (E)	Food/bait (t),	Range						
TOG	All others	(NI only)	all stocks offshore	of E_T	TOG	SC	GB	NI	RO	NS
				Fishing pattern I						
0.00	0.20	0.03	10 000 max.	<0.10	0.996	0.000	0.000	0.919	0.000	0.000
				0.10–0.19	0.004	0.000	0.000	0.073	0.000	0.000
				0.20–0.29	0.000	0.960	0.947	0.004	0.922	0.983
				0.30–0.39	0.000	0.032	0.046	0.003	0.062	0.013
				>0.39	0.000	0.008	0.007	0.001	0.016	0.004
				Fishing pattern II						
0.15	0.20	0.03	10 000 max.	<0.10	0.000	0.000	0.000	0.884	0.000	0.000
				0.10–0.19	0.940	0.000	0.000	0.110	0.000	0.000
				0.20–0.29	0.060	0.933	0.922	0.006	0.894	0.973
				0.30–0.39	0.000	0.057	0.065	0.000	0.081	0.023
				>0.39	0.000	0.010	0.013	0.000	0.025	0.004
				Fishing pattern III						
0.00	0.20	0.03	Entire surplus	<0.10	0.000	0.000	0.000	0.020	0.000	0.000
				0.10–0.19	0.998	0.000	0.000	0.287	0.000	0.000
				0.20–0.29	0.002	0.129	0.174	0.583	0.216	0.075
				0.30–0.39	0.000	0.591	0.525	0.097	0.452	0.711
				>0.39	0.000	0.320	0.301	0.013	0.332	0.214
				Fishing pattern IV						
0.15	0.20	0.03	Entire surplus	<0.10	0.000	0.000	0.000	0.656	0.000	0.000
				0.10–0.19	0.969	0.000	0.000	0.340	0.000	0.000
				0.20–0.29	0.031	0.922	0.885	0.004	0.865	0.978
				0.30–0.39	0.000	0.077	0.106	0.000	0.127	0.021
				>0.39	0.000	0.001	0.009	0.000	0.008	0.001

Effects of Mixed Stock Harvest

To simulate effects of mixed stock harvests on individual spawning stocks and inshore harvest levels, we examined four combinations of inshore and offshore fishing patterns (Table 5). Inshore commercial and subsistence harvests were taken from discrete spawning stocks; the offshore food/bait harvest was taken from mixed stocks of mature herring. Probability of overharvesting individual spawning stocks (where overharvest is defined as $E > 0.3$) was generally less than 0.06 when offshore fishing was limited to a 10 000 t maximum harvest (patterns I and II) or an amount equal to 5% of the Togiak surplus (pattern IV). In these cases, total biomass and mean sac roe and subsistence harvests for stocks other than Togiak were

similar to those obtained when $E = 0.2$ and no mixed stock fishery occurred (Fig. 4B, 4D; 5A, 5B, 5D). However, when no inshore harvest was taken from the Togiak stock and an amount equal to 20% of this spawning biomass was allocated offshore (pattern III), effects upon other (smaller) spawning stocks were dramatic (Table 5; Fig. 4C). Probability of overharvesting ($E > 0.30$) these smaller spawning stocks increased to 0.78 or more for all stocks except Nelson Island, which had a probability of overharvest of 0.11. A marked overall decline in inshore harvests from those obtained when $E = 0.2$ and no mixed stock fishery occurred was also shown for these groups (Fig. 5C). Effects of offshore mixed stock harvests were always greatest for the smallest spawning groups, which were already harvested at a constant inshore E of 0.2.

Conclusions

Although the computer model gives our best estimate of long-term consequences of different harvest strategies, simulation results must be used with caution. Pacific herring lack strong density-dependent regulatory mechanisms and are subject to large abundance fluctuations due to biotic and abiotic factors (Cushing 1981; Blaxter and Hunter 1982). Fishing may intensify or increase the possibility of stock declines. Since the model cannot be used to forecast events for a given year, management procedures must remain flexible to react to unforeseen abundance fluctuations.

Eastern Bering Sea herring stocks are still recovering from heavy exploitation that occurred during the peak of the foreign offshore trawl fishery (1968–77). Therefore, although maximum yield within the model was obtained at an E of 0.30, it may be prudent to maintain the current maximum E of 0.20. This may allow stocks to regain their former abundance more quickly and provide a measure of protection against overharvest, while only decreasing mean harvests by 7% and increasing mean spawning biomass by 52% from levels obtained at an E of 0.30.

During years in which the inshore fisheries fail to harvest the Togiak group at an E of 0.20, an offshore harvest to 10 000 t could be allowed with minimal risk to other spawning groups. While a somewhat higher offshore harvest could be taken during some years, it is necessary to restrict offshore (and inshore) mixed stock fisheries to lower levels than would be appropriate for fisheries targeting upon discrete stocks, since the risk of overharvesting individual stock components increases with size of harvest (Table 5).

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Recent Changes in the Central and Southern North Sea Herring Stocks[1]

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Burd, A. C. 1985. Recent changes in the central and southern North Sea herring stocks. Can. J. Fish. Aquat. Sci. 42(Suppl. 1): 192–206.

Since 1980 there has been a sudden recovery of recruitment to the central and southern North Sea herring stocks (Bank and Downs, respectively). In contrast, recruitment to the northern North Sea has continued at a low level and spawning stock biomass has even declined since 1979. These events underline the independence of the substocks in the North Sea, each of which has reacted differently to the cessation of the directed herring fishery in the North Sea since 1977. A precondition to the reopening of a herring fishery in the North Sea was that the severely depleted spawning stock biomass should have recovered to 800 000 t, the underlying assumption being that all components would respond in a similar manner and that a reopening of the whole North Sea would be possible. This has not happened and it may well be that management of the North Sea as a single unit is not a viable management procedure. The paper examines the historic changes in sizes of the Bank and Downs stocks, with particular emphasis on the most recent period. Evidence of density-dependent growth change is considered together with the recent data on fecundity and larval herring production. It is concluded that if the separate stocks are to be managed individually for maximum yield, then global North Sea regulations such as a total allowable catch and size regulation are inappropriate. Regulations must also take into consideration the seasonal distributions of the stocks. Indeed, this would lead, in particular, to more restrictive and specific regulation of the industrial fisheries.

Depuis 1980, le recrutement dans les stocks de hareng des parties centrale et méridionale de la mer du Nord (Bank et Downs respectivement) s'est soudainement rétabli. Par contre, le recrutement dans la partie septentrionale s'est maintenu à un faible niveau et la biomasse du stock des géniteurs a même baissé depuis 1979. Ces faits révèlent l'indépendance des sous-stocks de la mer du Nord, chacun ayant réagi différemment à l'arrêt de la pêche sélective du hareng depuis 1977. Une condition préalable à la réouverture de la pêche du hareng dans la mer du Nord était que la biomasse très affaiblie du stock de géniteurs atteigne 800 000 t, un rétablissement basé sur les hypothèses selon lesquelles toutes les composantes réagiraient de façon semblable et une réouverture de la pêche dans toute la mer du Nord serait possible. Comme cela ne s'est pas réalisé, il est bien possible que la gestion globale de la mer du Nord ne constitue pas une méthode gestionnelle viable. L'auteur examine les variations antérieures de la taille des stocks Bank et Downs, en insistant sur la période la plus récente. Il étudie aussi les changements au niveau de la croissance dépendante de la densité, en plus des données récentes sur la fécondité et la production de larves de hareng. Si les différents stocks doivent faire l'objet d'une gestion individuelle pour un rendement maximal, l'auteur conclut qu'il ne convient pas d'adopter des mesures portant sur toute la mer du Nord, comme le total de prises allouées et la limite de taille. Les mesures doivent aussi tenir compte des répartitions saisonnières des stocks. De fait, cela mènerait en particulier à une réglementation plus précise et plus restrictive des pêches industrielles.

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Descriptions of the long-term changes in the age composition of the North Sea stock, and accounts of scientific disputes that arose in attempting to introduce conservation measures, are given in Burd (1978); that review was updated and extended to include the west of Scotland fisheries by Saville and Bailey (1980).

Managers and scientists failed to take action to prevent the collapse of the southern North Sea (Downs) stock in the mid-1960s because of the problem of quantifying the catches of that stock made in the fisheries in the central and northern North Sea. This collapse was followed by a sudden expansion in the fishery in the entrance to the Skagerrak, where the fishery collapsed in 1970, to be followed quickly by those in the central and northwestern North Sea. The locations of current North Sea spawning grounds and the International Council for the Exploration of the Sea (ICES) Statistical Divisions are shown in Fig. 1.

In 1969, the North-East Atlantic Fisheries Commission (NEAFC) considered introducing national herring quotas, but found that due to the forms of national legislation the legal administrative requirements for such action would be long in implementation. An interim solution was sought, and in 1970,

[1]This paper was presented at the International Symposium on the Biological Characteristics of Herring and Their Implication for Management, convened at Nanaimo, B.C., June 20–22, 1983, commemorating the 75th anniversary of the Pacific Biological Station.

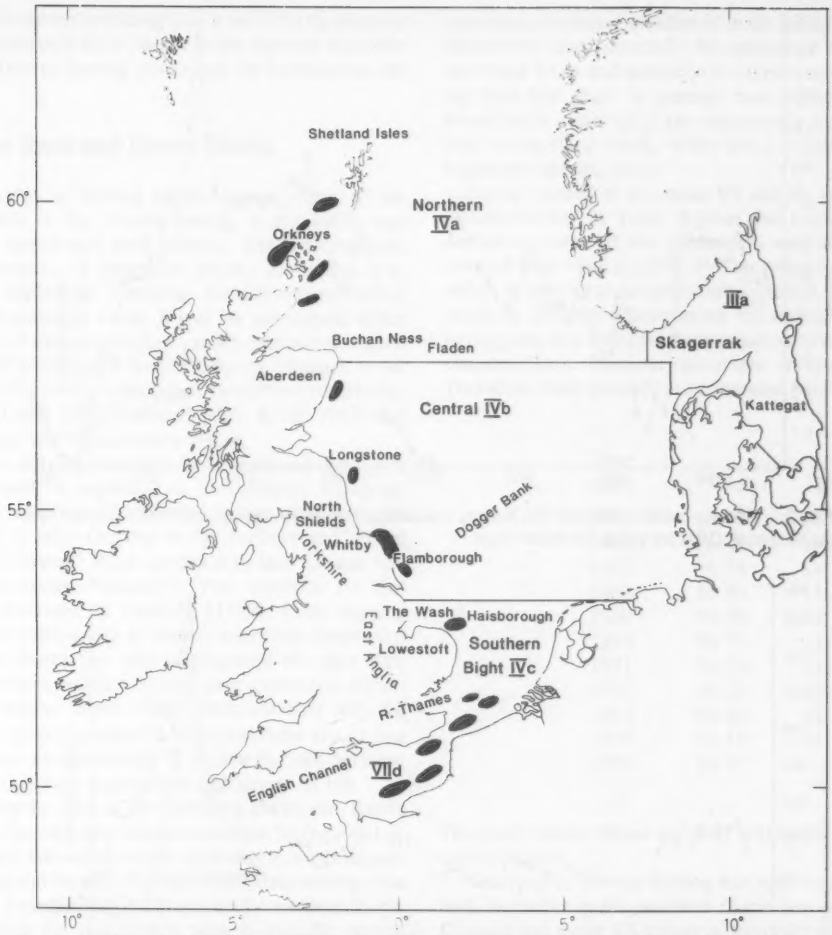

FIG. 1. Location of current herring spawning grounds in the North Sea and eastern English Channel. ICES Statistical Divisions are indicated (Roman numerals). Bank herring spawn in IVb from July to October and include the Flamborough spawning. Downs herring spawn from November to February. (Redrawn from Posthuma et al. 1977)

bans on North Sea and Skagerrak herring fishing in the month of May and from 20 August to the end of September were agreed to by NEAFC. This regulation came into force in 1971. Over the next few years the extent of these closures was increased but failed to control the levels of fishing mortality. A regulation by annual total allowable catch (TAC) was agreed to in 1974 and the seasonal closure was allowed to fall into abeyance in 1975 (Saville and Bailey 1980). However, the United Kingdom unilaterally introduced a ban on fishing within its fishing limits off the Yorkshire coast between 20 August and 30 September, when the herring were on the spawning ground. This ban has been enforced up to the present.

In its 1975 Liaison Committee Report, ICES recommended a total ban on herring fishing in the North Sea (Anonymous 1977a). This extended the unanimous resolution of NEAFC in 1975 to ban industrial fisheries for herring. Nevertheless, NEAFC adopted a TAC of 160 kt (160 000 t) for 1976 and agreed to a minimum landing size of 20 cm aimed at restricting the fishery for juvenile herring. The 1976 catch reached 175 kt despite a unilateral ban on directed herring fishing within United Kingdom fishery limits from October to December. This ban was reintroduced in March 1977. Eventually, following the extension of the limits of fisheries jurisdiction and the agreement between Norway and the European Community, a total ban on fishing for herring in the North Sea (ICES Subarea IV) and the eastern English Channel (ICES Division VIId) was imposed in February 1977 and maintained until October 1981. Despite this ban, herring have been taken as "by-catches." Much of these have come from the industrial fishery for sprat where large numbers of 0-group herring have been taken.

Herring fishing continued in the Skagerrak and Kattegat (ICES Division IIIa) at a level of about 100 kt annually. Much controversy has occurred over the effect of this uncontrolled fishery on the rate of recovery of the North Sea spawning stocks.

The historic levels of catches of herring from the North Sea (excluding the Norwegian spring spawner fishery) are shown in Fig. 2. In 1936–37 and 1947–51, when the catch was about 500 kt, the average fishing mortality was approximately 0.25 and the spawning stock biomass averaged 2.4 million t (Burd 1978). By 1975 the spawning stock biomass was reduced to 0.24 million t, with annual fishing mortalities in excess of 1.0 during the preceding 5 yr. The spawning stock biomass in 1983

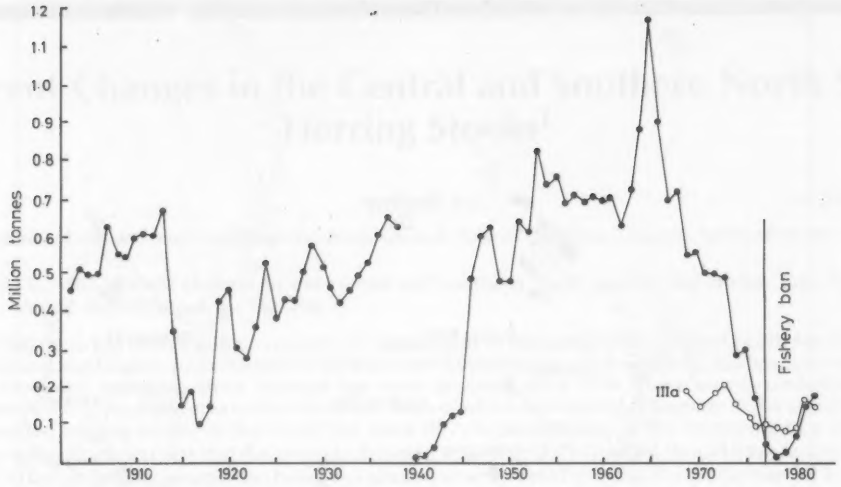

FIG. 2. Historic catches of North Sea herring (excluding Norwegian spring spawners). Catches from the Skagerrak (IIIa) are given for recent years.

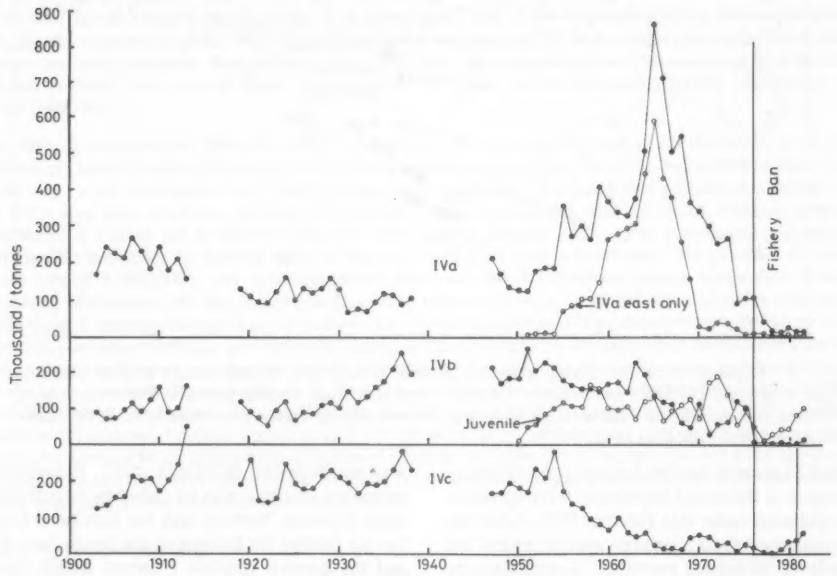

FIG. 3. Catches of herring by ICES Division.

has recovered to about 800 kt, and though some limited catches have been allowed in 1982 and 1983, the stock is far below the level giving the historic stable yield of 500 kt.

Lack of enforcement of regulation has allowed herring catching to continue during the ban and the 1981 TAC to be exceeded. In Fig. 3 the area breakdown of the catches shows that the major increase derives from by-catches of juveniles in IVb, which have now returned to the level of 100 kt that existed before the fishing ban. In IVc the stock recovery in 1980 was marked by an illegal fishery on the Southern Bight and English Channel spawning grounds of about 40 kt. In 1981 the fishing ban in IVc was ended; a TAC for this area was set at 20 kt and a catch of 42 kt was taken. The 1982 TAC of 72 kt was taken by uncontrolled but limited fishing effort.

The scientific criteria that should be met to enable the ICES Advisory Committee on Fishery Management (ACFM) to recommend reopening of the North Sea fishery were defined by the ACFM (Anonymous 1980, 1981a, 1983a). A reopening could be considered when evidence was available to show that (1) the total North Sea spawning stock biomass had recovered to 800 kt and would continue to increase under moderate fishing and (2) there was evidence of increased recruitment. These criteria were formulated in accordance with the practice of treating the North Sea herring as a single stock unit for management purposes. It was clear by 1981 that the North Sea component spawning stocks were not responding uniformly to the closure. In recommending a reopening of the fishery in IVc in 1981 and 1982 the ACFM recognized that the North Sea

herring population cannot be managed as a unit. It is the purpose of this paper to reexamine the evidence of the separate identities of the Bank and Downs herring stocks and the implications for management.

Identities of the Bank and Downs Stocks

The establishment of fishing as the causal effect of the reduced catch rates in the Downs herring in the 1960s was dependent on the question of stock identity. The proof required to persuade managers to introduce fishery restriction was confounded by arguments implying natural environmental changes being the possible cause. It was the assessment of the causes and effects of increased annual growth rate on maturation and recruitment (Cushing and Burd 1956) and changes in the distributions of the location of catches in the northwestern North Sea (Parrish and Craig 1963; Schubert 1963; Krefft 1963) that led to the failure to take conservation action.

For many years, herring biologists had considered that North Sea spawners could be regarded as two distinct biological groups (Anonymous 1936). The "Bank" herring stock included all fish spawning in July–October in the northern and central North Sea. The "Downs" stock spawned in late autumn and early winter (November–February). The evidence for this distinction was reviewed by Cushing (1955). From tagging studies he showed differences in annual migration patterns of the adults in the North Sea and summarized the data then available on vertebral number, which give consistent differences between stocks. Burd (1962) demonstrated that the growth in the first year (l_1) also characterized these stocks and that any differences at recruitment in l_1 distributions between stocks in a year class were maintained throughout its life.

However, during the 1961 ICES Herring Symposium, Krefft (1963) suggested that the two stocks could not be regarded as self-contained units but could switch spawning grounds dependent on environmental factors. Zijlstra (1963), examining data on spawning fish from the Dogger Bank and the southern North Sea, concluded that the consistency seen in growth, otolith characters, and vertebral counts suggested "homing" of recruits to their place of origin.

Meetings of ICES Working Groups in 1961, 1962, and 1963 examined all available data on stock discrimination and distinguished three spawning groups, splitting the previous "Bank" into the Buchan stock and the Dogger Bank stock (Anonymous 1965). The Buchan stock included spawnings from July to early September stretching from the Shetland and Orkney Islands and down the Scottish east coast. The Dogger Bank stock included fish spawning around the Bank itself and also the English coastal grounds. The term "Bank" stock has been used in this more restricted sense subsequently. Cushing and Bridger (1966) described the migration circuits of the three stocks as deduced from tagging returns and other evidence.

The controversy over stock identity was not ended, as Schumacher (1967), based on an analysis of gill rakers only, suggested that Bank herring consisted of a mixture of the pure Buchan and Downs stocks. Zijlstra (1969) refuted this hypothesis and again stressed his homing belief but agreed with Harden Jones (1968) on the need for more proof.

A number of the year class characters are summarized in Table 1. As herring spawn from July to March, the year classes are designated by season, e.g. July 1948 to March 1949 as 1948–49. The meristic characters used are of a phenotypic nature and may reflect differences in temperatures on the spawning grounds or conditions in the nursery area. The growth differences may primarily be generated from the different spawning times and subsequent environmental conditions during their first year. In general, both vertebral sum (VS) and keeled scale count (K_2) are consistently higher in the Downs than in the Bank stock, while the l_1 values and hence mean length per age are lower.

Casual perusal of the mean VS and K_2 values for Bank and Downs herring in Table 1 gives the impression of a steady decline in value of the parameters over the 30 year classes covered from 1948 to 1979. It is tempting to suppose that these reflect a long-term environmental change. Such a conclusion could be illusory. These mean VS and K_2 are derived from aggregated data collected from numbers of individual spawning concentrations. Meristic characters collected only from the Yorkshire coast grounds are compared below:

Year class	VS	K_2
1965	56.13	14.30
1966	56.42	14.23
1967	56.54	14.55
1968	56.50	14.86
1969	56.58	14.76
1970	56.33	14.44
1971	56.29	14.15
1972	56.28	14.45
1973	56.26	14.21
1978	56.18	14.13
1979	56.47	—

The most recent values are well within the range observed in earlier years.

Historically, Downs herring that spawned in late November and December in the southern North Sea and eastern English Channel had mean VS values of the order of 56.5–56.6, while those spawning in January and February in the eastern English Channel usually had values greater than 56.7. As the Downs stock declined, the fishery became more concentrated in November and December. In January 1980, a major production took place in the eastern English Channel on the traditional spawning area. It is perhaps significant that the 1979–80 year class showed an increase in mean vertebral count compared with earlier year classes when little spawning took place in those areas (1970–78).

Characters relating to reproductive capacity also distinguish Bank and Downs herring. Baxter (1959) examined fecundity in the two groups. Because of the chances of eggs having already been released, Bank and Downs herring in actual spawning condition cannot be used in such a study, but counting must be made on fish as close to spawning as possible, i.e. in maturity stages IV and V. Iles (1964) pointed out that there was no easy way that a fish in stage V sampled in September or October in the central North Sea could be identified as a Bank or Downs spawner. Selection of suitable fish for analysis is therefore critical, and there is considerable doubt as to the allocation of fish to stock in much published material.

As fecundity is length (or weight) dependent and as length itself is a discriminant character of a year class, Burd and Howlett (1974) defined the stock differences in terms of a fecundity index (fecundity/total length cubed). The indices

TABLE 1. Comparison of meristic characters of various year classes of Bank and Downs spawners (mean values).

Year class	Bank			Downs			Source
	l_1 (cm)	VS	K_2	l_1 (cm)	VS	K_2	
1948–49		56.48			56.63		Cushing 1955
1949–50		56.45			56.63		
1950–51		56.50			56.58		
1952–53	14.59	56.54		13.17	56.64		Zijlstra 1969
1953–54	14.60	56.61		11.73	56.72		
1954–55	14.20	56.47		12.35	56.59		
1955–56	15.32	56.66		13.82	56.64		
1956–57	12.40	56.45		11.08	56.61		
1957–58	14.20	56.46		12.74	56.62		
	14.02	56.47	14.79	12.58	65.61	15.04	Anonymous 1969
1958–59		56.41			56.69		Zijlstra 1969
	15.76	56.38	14.79	12.73	56.64	14.88	Anonymous 1969
1959–60		56.36			56.41		Zijlstra 1969
	15.53	56.34	14.54	13.75	56.45	14.95	Anonymous 1969
1960–61		56.41	14.60		56.48	15.05	Zijlstra 1969
	15.94	56.39	14.78	12.79	56.47	15.14	Anonymous 1969
1961–62	13.97		14.69	13.32		14.84	Zijlstra 1969
1965–66		56.21	14.45				Fisheries Laboratory, Lowestoft
1966–67		56.43	14.42		56.74	14.91	
1967–68		56.46	14.39		56.65	14.44	
1968–69		56.45	14.70				
1969–70		56.44	14.58		56.44	14.25	
1970–71		56.35	14.40		56.47	14.58	
1971–72		56.30	14.16				
1972–73		56.33	14.36				
1973–74		56.35	14.11				
1974–75		56.32	13.32		56.47	14.32	
1975–76		56.41	14.25		56.52	14.25	
1976–77		56.29	14.03				
1977–78		56.28	13.87		56.33	14.45	
1978–79		56.31	14.16		56.53	14.30	
1979–80		56.49	14.17		56.64	14.33	

NOTE: l_1 is the back-calculated length when the first winter ring is laid down on the fish scale; VS is the total number of vertebrae in the backbone including the urostyle; K_2 is the number of keeled scales in the ventral mid-line between the gills and the anus.

derived were as follows:

Age (yr)	Downs		Bank	
	Mean	SD	Mean	SD
3	14.81	2.49	27.58	4.84
4	17.13	3.17	36.91	6.62
>4	19.67	3.97	40.49	6.68

It has been supposed that with change in age of first maturity and the big increase in mean length for age, fecundity of the fish might also have increased. In August 1982, gonads were collected by research vessel from coastal grounds off Whitby and Scarborough when both Bank and Downs herring would be expected to be present. The earlier pure Bank and Downs regressions on which the 1982 data have been plotted are shown in Fig. 4. High maturity stage fish must be Bank herring, and low maturity fish must be Downs herring. The data points are seen to fit the regressions. Evidently the basic fecundity–length relationship has been maintained despite the changes in growth and biomass.

Hempel and Blaxter (1967) surveyed herring egg weights from the northeast Atlantic region, and Zijlstra (1969) showed consistent differences for Bank and Downs herring. The two series of data are given in Table 2. Combination of the two stock characters egg weight and fecundity index clearly discriminates between individuals of the two stocks (Fig. 5).

Greer Walker et al. (1972) showed that the total numbers of white skeletal muscle fibres differed significantly between Bank and Downs stocks (Table 3). Though there is no clear evidence in fish that this character is genetically determined, Luff and Goldspink (1970) have shown such a dependence in mammals.

Comparison of the racial characters for Bank and Downs herring between the recent and earlier years shows that there has been little or no change in any of the parameters examined. In the case of fecundity this is despite a large increase in growth. Though environmental factors have been cited as responsible for changes in the abundance and distribution of the two stocks, the evidence presented here would suggest that the separate identity of the stocks has been unchanged. One is led to the conclusion that this must be maintained by a positive mechanism. Homing of recruits to their place of origin would be the simplest explanation. Kamp and Corten (1982) suggested that the loss of the Dogger Bank component of the Bank stock might have been caused by environmental factors reducing larval herring survival. However, the extinction of a genetically

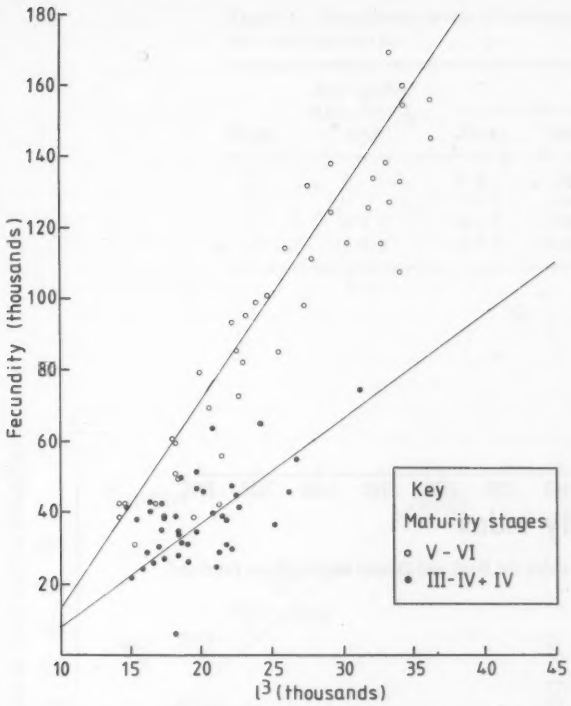

FIG. 4. Fecundity–length regressions of Bank and Downs stocks. Individual points show observations made in August 1982 on catches off the English northeast coast.

TABLE 2. Bank and Downs stock egg weights.

Year class	Bank mg/100 eggs	*n*	Downs mg/100 eggs	*n*	Source
1956 1957	22.71	44	37.50	26	Hempel and Blaxter 1967
1958	20.26	9	35.77	10	Zijlstra 1969
1960	19.21	27	35.25	88	
1961	21.80	19	35.03	63	
1962	21.04	29	35.25	10	
1963	19.99	34	34.43	16	

determined local stock by fishing might equally well account for the failure of that component to recover.

Mixing of the Bank and Downs Stocks

The fact that recovering spent Downs herring migrated back from the southern North Sea spawning grounds through ICES Division IVc during February and March was well established in pre-war years, when a regular fishery occurred. They passed into the western central North Sea IVb during the spring and spread northwards over these rich feeding areas during the summer. Their return migration south accelerated during July, August, and September.

During the period 1930–33 Hodgson attempted to give qualitative forecasts of the recruiting 2-ringers to the southern North Sea fishery based on their presence in the North Shields fishery. Because of the low growth rate at that time, recruitment was spread over 2-, 3-, and even 4-ringers, dependent on the timing of their reaching the length of first maturity (Burd 1962). In that paper I examined the relationship between the catch per unit effort (CPUE) of herring landings in East Anglian ports of Lowestoft and Great Yarmouth and the sequential monthly CPUE data from the mixed stock fishery at North Shields in the same and in the next year. The results are summarized in Table 4 from which the mixing of Downs herring can be assessed.

The 2-ringed North Shields fish were mainly immatures and were not correlated with the 2-ringed fish recruited in the same year to the adult stock in East Anglia. However, abundance indices of the 2-ringers from the East Anglian fishery in year *n* were correlated with the CPUE values in the Shields fishery the following summer (year $n + 1$). Positive correlations in May and June existed between the CPUE indices of 3-ringers in both fisheries in the same year: in July to September there was a gradual concentration of the North Shields fishery in the vicinity of the spawning grounds of the Bank herring, which accounts for the lack of correlation in CPUE data with East Anglian abundances later in the same year. A high correlation existed between the 3-ringers in the East Anglian fishery and those in the fishery off North Shields the following May when the catches consisted mainly of recovering spent herring.

In 1950 a sharp increase in abundance of *Calanus* was observed in the North Sea, and increased growth rate of the herring resulted in a change of the age at first maturation (Burd 1963). As a consequence, full recruitment of a year class took place as 2-ringers, and the relationship between the North Shields CPUE index and that in East Anglia also changed.

For a number of years, until the collapse of the North Shields and East Anglian drift net fisheries, forecasts of the abundance of 2-ring recruits were made on the basis of the CPUE of fish below maturity stage IV in July in the North Shields fishery (Fig. 6). Close correlation was also obtained between the abundances of 2- and 3-ringed fish in maturity stage IV and above in July and the CPUE of catches taken in the spawning fisheries of the Bank herring in August–September off the Yorkshire coast (Fig. 7a and 7b).

With the collapse of the drift net fisheries in the North Sea, the only long-time series of CPUE data ended. The directed nature of the fishing using echo sounders and the rapid changes in trawl design, both bottom and pelagic, has limited the use of CPUE as an abundance index for Bank and Downs stocks. A major part of the catch was also taken by purse seine. The drift-net catches representing an insignificant part of the total could no longer be regarded as representative of the total catch either in age composition, location, or seasonality.

The advice on herring stock management could no longer be offered on a stock by stock basis, and consequently, in 1971 the ICES Herring Assessment Working Group (Anonymous 1972) decided to treat the North Sea herring as a single population in virtual population analysis (VPA). However, in so aggregating the catch data on an annual basis, information relevant to the changing exploitation pattern on the different stock components was lost. For example, the traditional northwestern North Sea fishery off the Scottish coast had been the main fishery in IVa. A sudden expansion of the purse-seine catches in the eastern half of IVa took place about 1960. When this fishery collapsed in 1970, vessels turned to areas to the west of the Orkney and Shetland Islands which maintained the total catches in IVa but

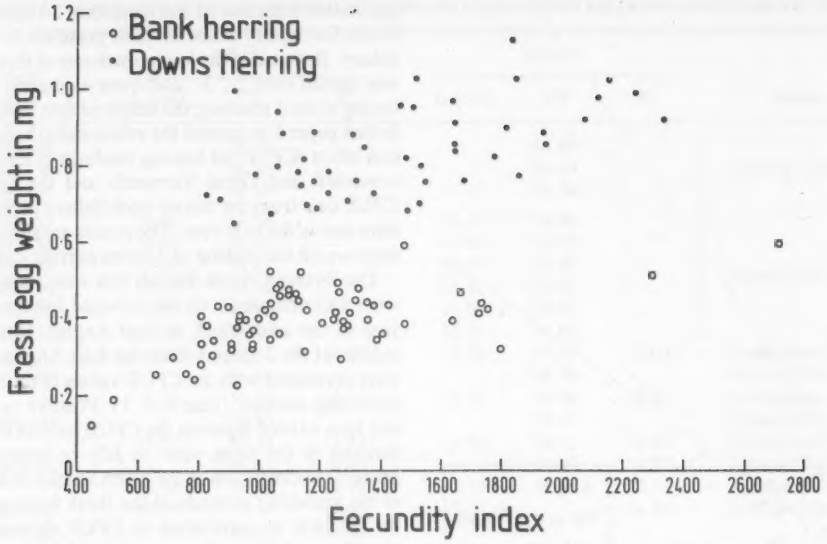

FIG. 5. Relation between egg weight and fecundity index for Bank and Downs herring (from Burd and Howlett 1974).

TABLE 3. Mean white fibre numbers for North Sea spawning herring.

	Year	Number	Standard error
Bank	1969	63 842	± 702
	1970	64 976	±1102
Downs	1969	40 236	± 944
	1970	40 861	± 713

masked the events in the traditional North Sea fisheries. The total North Sea assessment by VPA was continued up to the closure of the fishery in 1977. The management actions as a consequence of these annual assessments are described in the introduction.

Following the introduction of the ban on herring fishing in the North Sea, monitoring the North Sea stock relied upon the changes in larval herring abundance at spawning time (a reversion to individual stock assessment) and estimation of total 1-group recruitment in the North Sea.

In an attempt to follow the decline of the Downs stock, Burd (1973) presented VPA biomass estimates for the three Divisions of the North Sea separately, based on catch data from a 24-yr period. As only Downs herring occur in Division IVc, but are also caught earlier in the year in the northern fisheries, this biomass estimate represents a minimum estimate of Downs stock. Average mixing rates of Downs herring in IVb were obtained and tentative stock and recruitment plots were given for Downs and Bank herring. Andersen et al. (1974) extended the use of the Division VPAs, based on a model defining the annual residence period of Downs herring in the three North Sea Divisions.

Wood and Burd (1976) showed that the larval herring indices for the Bank stock for the period 1967–73 were highly correlated with the VPA spawning stock biomass for IVb. The ICES Working Group on North Sea Herring Larval Surveys in 1976 (Anonymous 1977b) adopted this procedure to derive

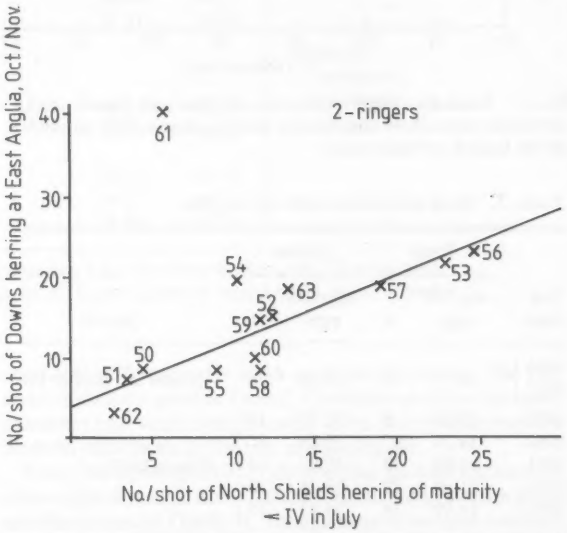

FIG. 6. Regression used for prediction of East Anglian drifter catch per shot of 2-ringers based on North Shields drifter catch per shot of fish of maturity below stage IV.

VPA estimates of the IVa, IVb, and IVc spawning stocks (Buchan, Bank, and Downs, respectively). The ICES Herring Assessment Working Group and the Working Group on Herring Larval Surveys (Anonymous 1981b) later examined the nature of these correlations and made adjustments to the catches in the VPA data base to account for the occurrence of catches of Downs herring in IVb.

More recently, acoustic surveys at Shetland, the Yorkshire coast, and in the Downs spawning area have been used to assess stock size. Thus, the present assessment of the total North Sea herring stock is once again dependent upon the derivation of individual stock estimates.

TABLE 4. Significance levels of correlation coefficients of CPUE by months, 1927–38 (ns = not significant).

Rings	East Anglia (Oct.–Nov.), year	North Shields					
		Year	May	June	July	August	September
2	n	n	ns	ns	ns	0.02	ns
2	n	$n+1$	ns	0.01	0.01	0.02	ns
3	$n+1$	$n+1$	0.01	0.001	0.02	ns	ns
3	$n+1$	$n+2$	0.001	ns	ns	ns	ns

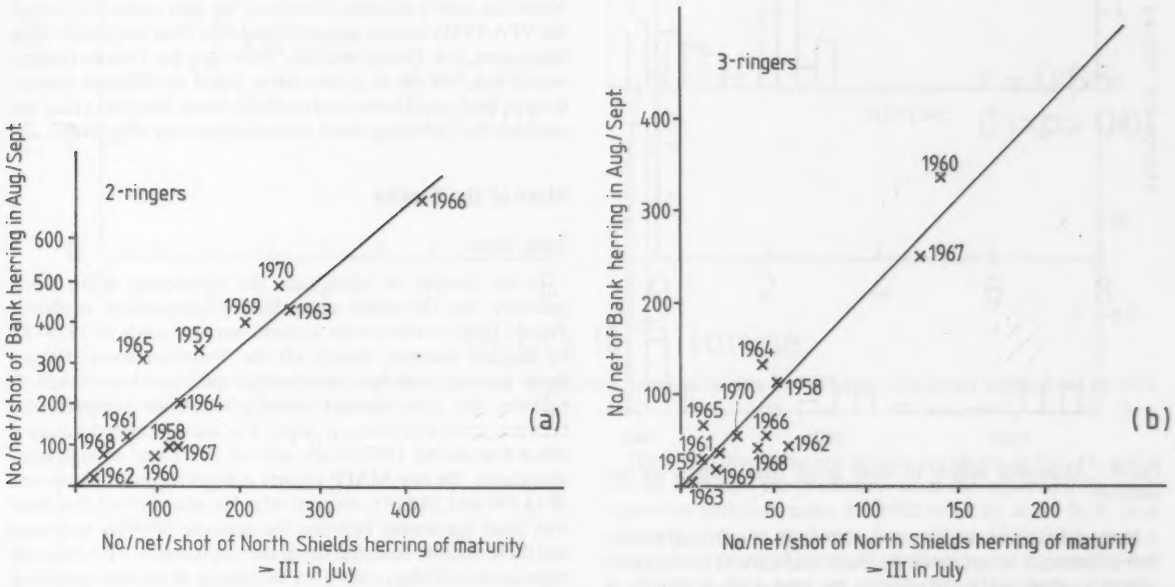

FIG. 7. Regression of number per drift net per shot of Bank herring at Whitby in August–September on high maturity stage fish in July North Shields catches. (a) 2-ringers; (b) 3-ringers.

Recruitment to the Bank and Downs Stocks

Evidence from Larval Surveys

The larval herring abundance indices for IVa and Bank and Downs stocks are shown in Fig. 8. In IVa the NEAFC spawning period closure became effective in 1972, and it is tempting to suppose that the increased larval production was a direct consequence giving a temporary respite to the adult stock. Following the high larval production in 1978 successive numbers have declined.

Major reduction in fishing effort in the English coast spawning areas in IVb only occurred after 1971. Again it is attractive to associate the high production of larvae with the protection of the spawners. The Downs larvae showed a spectacular increase in 1981.

The changes in larval numbers and estimated spawning stock biomasses have been somewhat loosely used to project trends in likely recruitment to the individual stocks. The first indication of year class strength is obtained from the 0-group herring surveys made annually along the English east coast (Wood 1983). These commenced in 1953 but from 1967 they have been conducted with a standard midwater trawl at fixed stations each year. Downs 0-group herring (identified by otolith types, vertebral number, and keeled scale counts) are distributed in summer along the coasts of East Anglia and the Thames Estuary. Bank herring (similarly identified) occur to the north, with increasing numbers of IVa recruits in the most northern sector.

Wood (1983) showed that the estimates of Downs 0-group herring were highly correlated with VPA 2-ring recruits of the Downs stock when the two periods before and after the ban on juvenile herring fisheries were taken separately. The predictive value is greater when the stock is not heavily exploited between the 0-group estimate and its recruitment to the adult stock. Nevertheless, in both periods the 0-group estimate clearly reflects year class strength as adult recruitments.

The Downs larval index may also provide some index of year class strength. As the 0-group estimate is made before any significant catches are taken from the year class, it may be considered to represent a preexploitation estimate of year class strength as is the larval estimate. The correlation between the two estimates is shown in Fig. 9a.

Indices of Bank 0-group have been taken from the area south of Flamborough Head to the Wash. This choice is made in order to minimize IVa recruitment affecting the estimate. These indices have been correlated on the Bank larval estimates (Anonymous 1981b) (Fig. 9b).

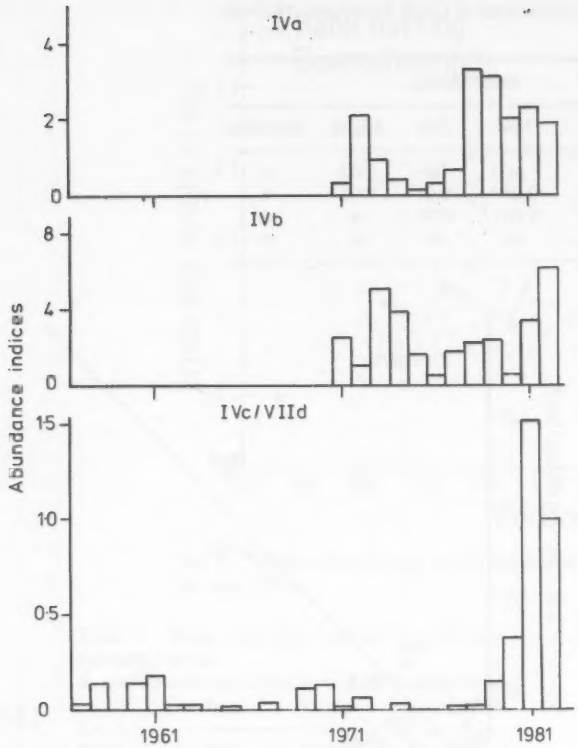

FIG. 8. Abundance indices of small larvae (note: indices are not additive).

Both correlations are significant, though at different levels. The differences in nature of the Bank and Downs correlations probably reflect real differences in the period when year class strength is established. The average age of Downs larvae in the index is about 30 d from egg deposition. The larvae hatch out in winter when food availability may be low and patchy. The period for commencement of feeding is critical, and in recent years, large numbers of yolk sac larvae taken in the surveys appear to have produced no older larvae. Those larvae surviving the initial mortality are drifted into the southern North Sea at a time when the spring outburst is commencing. Year class strength could well be determined at this early stage.

In contrast, Bank larvae hatching in the autumn are able to take advantage of the autumn production, and mortality in the early larval stages may not be so great. The Bank larval average age in the surveys would be about 20 d from egg deposition. These larvae, however, have the hazard of overwintering in the open North Sea before entering the coastal areas in May. Year class strength might well be greatly influenced by mortality during the winter.

Evidence from 1-Group Surveys

During the spring and autumn of 1960 and 1961, international young herring surveys were undertaken in the North Sea. The objectives were to identify the main centres of abundance of the prerecruits of the Bank, Downs, and Buchan stocks (Anonymous 1969). Though the analysis, using vertebral and keeled scale counts and growth data, was successful to a certain extent, it was clear that there was no easy way of identifying the components of young herring in the central North Sea. From these surveys the ICES International Young Herring Survey (IYHS) was developed, which provides estimates of total 1-ringed herring as in the North Sea (Fig. 10).

The 1-group herring in the North Sea include numbers of fish migrating from areas to the west of the Orkney and Shetland Islands. Herring tagged in the eastern North Sea as 1-group have been recovered in later years from fisheries to the west of Scotland (Anonymous 1975). This, incidentally, implies a well-developed homing mechanism. As these immigrants form a different proportion each year and occur in the juvenile herring catch, the VPA 1-group stock number overestimates potential North Sea native recruits. However, the data series over which the VPA/IYHS indices are correlated date from the period when there were few Downs recruits. Now that the Downs stock is recovering, the use of a correlation based on different proportions of Bank and Downs and northern North Sea stocks may not estimate the spawning stock recruitments very effectively.

State of the Stocks

Bank Stock

In the absence of catch data, the monitoring of the stock recovery has depended upon fishery-independent methods. Wood (1982) reviewed the acoustic surveys made in 1979–81 by English research vessels off the Yorkshire coast. During these acoustic surveys considerable care has been taken to calibrate the echo-sounder systems to ensure comparability between years and between ships. It is not considered a chance effect that during 1982 in one area of 102.1 km^2 of high echo abundance, the two MAFF vessels at night recorded biomasses of 14 494 and 14 814 t, respectively. He also showed that there was good agreement between the acoustic biomass estimates and those derived from the larval herring number/VPA biomass regressions and that, over 3 yr, the timing of the first spawning wave occurred 5–7 d after the new or full moon at the end of August.

The date of first spawning wave can be identified either from in situ catch data or from the subsequent release of small yolk sac larvae. At prevalent temperatures larvae appear at about 12–14 d after egg deposition. The timings of the first spawning waves in relation to the date and state of the moon are given in Table 5.

The age compositions and acoustic biomasses for the Yorkshire coast spawning are given in Table 6. No acoustic biomass is presented for 1980 because in that year the survey was timed too early for peak spawning. The high increment in biomass in 1982 was due to the strength of the 1979–80 year class, which, as larvae, was not as abundant as the 1974–75 year class (Fig. 8). Until 1982 the stock had been dominated by the survivors of the latter year class (7-ringers in 1982).

The acoustic biomass estimates only refer to a restricted period and area of Bank spawning. The ICES International Herring Larval Survey allows an assessment to be made of the proportion of the total Bank larval production that is generated in the acoustic survey area. Thus, Wood and Johnson (1983a) concluded that in 1982 the total spawning stock from the English northeast coast alone was about 74 kt. The ICES Herring Working Group (Anonymous 1983b) noted that an additional substantial spawning took place off the Scottish east coast and from the larvae production estimate calculated that about 43 kt may have spawned in the area.

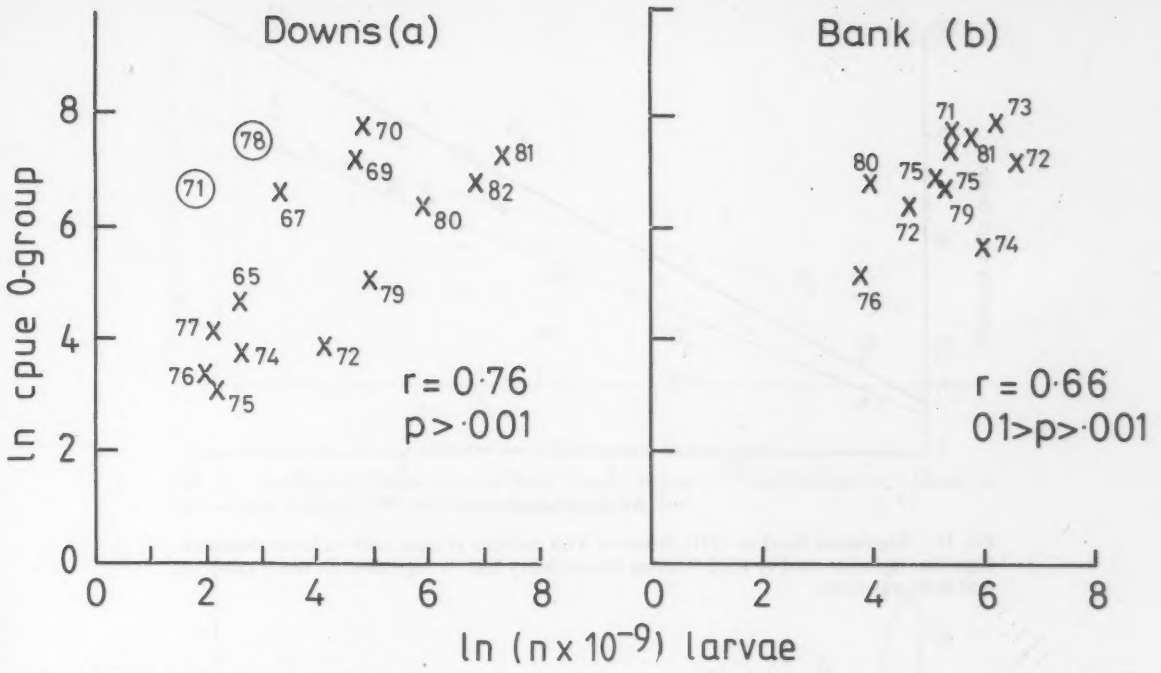

FIG. 9. Correlation of 0-group index on larval abundance. (a) Downs stock (note: larval data for 1978 year class poorly sampled and for 1971 year class underestimated); (b) Bank stock.

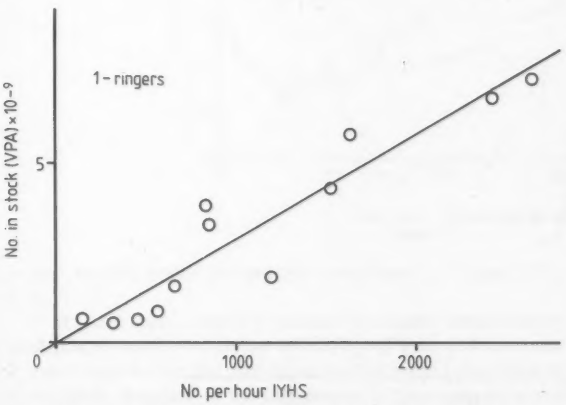

FIG. 10. Relation between VPA stock index and ICES IYHS abundance index.

A 1982 biomass of 100 kt has been used to initiate a VPA series to describe changes in Bank stock. As indicated under Mixing of the Bank and Downs Stocks, catches of herring in IVb contain varying quantities of Downs herring. In principle, these fish should be deducted from the catches used for VPA calculation of Bank herring. The data on maturity stages on which such an adjustment has been made are far from adequate. The utility of this adjustment has been examined by comparing the estimated spawning stock biomasses derived from the total IVb catch data and the IVb catch data adjusted to "exclude" Downs herring. The regressions for prediction of spawning stock biomass are calculated for the years 1971–76 when fishing still took place.

These two predictive regressions are shown in Fig. 11, and it can be seen that the prediction from the adjusted IVb catch regression underestimates the 1982 stock by about 30%. It is concluded that the prediction from adjusted IVb VPA gives a poorer description of recent stock changes and is probably due to the poor data base on which the adjustment is made. Consequently, in the long-term analysis of the Bank stock used here, the Division IVb catch data are utilized to generate stock sizes and are thus identical to those given in Burd (1978).

In the long term, i.e. 1947–82, the Bank stock biomass has fluctuated over an order of magnitude. Concurrent with this, there have been large changes in mean length. Age of recruitment to the stock has changed, becoming earlier as the fish grew quicker. The 3-ringed fish have been fully recruited to the stock throughout the period, and their mean values probably best reflect the magnitude of the growth changes. The mean lengths of both 2- and 3-ringers are shown in Fig. 12. The data from 1978–81 are derived from research vessels, as no commercial fishery was allowed. The quantity of data is

TABLE 5. Date and state of moon and timing of initial spawning.

Year	Moon		Spawning,
	Date	State	date
1979	22 August	New	27 August
1980	27 August	Full	1 September
1981	15 August	Full	22 August
1982	19 August	New	26 August
1983	23 August	Full	27 August

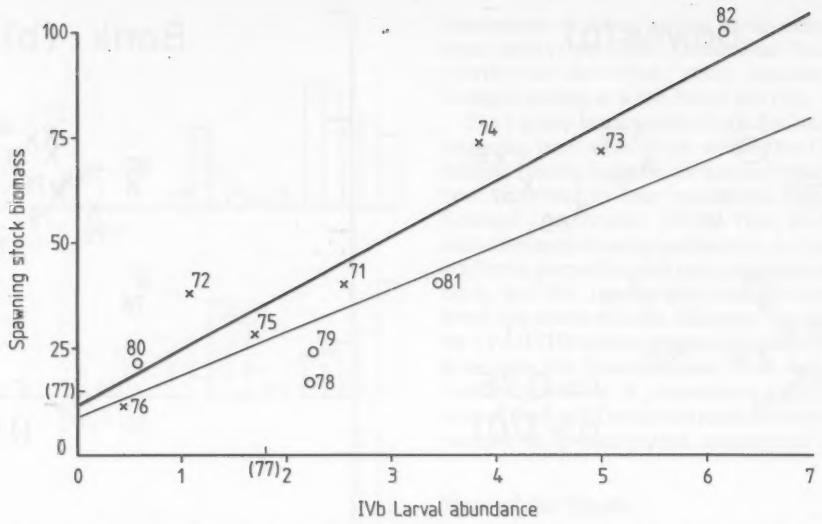

FIG. 11. Regressions based on 1971–76 data of VPA estimates of Bank stock on larvae abundance. Light line: regression used by ICES Working Groups; heavy line: ×, regression; ○, recent values not used in the regression.

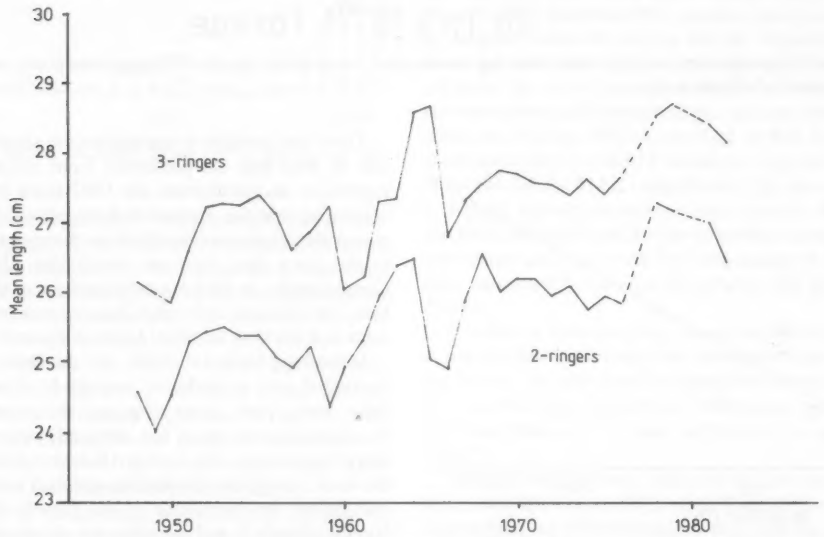

FIG. 12. Mean lengths of 2- and 3-ring Bank spawners.

somewhat limited and probably has a high variability, except in 1982. Up to 1972, all data are from the English fishery; for 1972 onwards, Dutch and French scientists have provided information that amplifies the data from English research vessels.

The changes in mean length at age can be interpreted in relation to two factors: firstly, the sudden increment in *Calanus* in the 1950s, and secondly, the declining herring biomass in the 1960s and 1970s. The initial growth increment was shown by Burd (1963) to be associated with a doubling of the *Calanus* population after 1950. This outburst in *Calanus* production was maintained until the mid-1960s, but since then the abundance has steadily declined (Bainbridge et al. 1978). Though the *Calanus* increment of the 1950s had a real effect in boosting growth (Iles 1971), the trend in growth shown in Fig. 12 represents part of a long-term trend (see Fig. 14).

The mean length at any age represents the cumulative effects of the growth history. At the length of first maturity (approximately 22 cm) the herring has already achieved some 70% of its total potential growth. Thus, the mean length of recruited fish is to a great extent determined by growth in their first and second years. As 0-group, the young fish are initially distributed in shallow coastal areas. Bank herring being spawned earlier than Downs herring have an initial length advantage. Iles (1971) considered that the low mean l_1 in the post-war year classes was a reflection of intraspecific competition: "the full realization of the growth potential of all surviving members of the year class

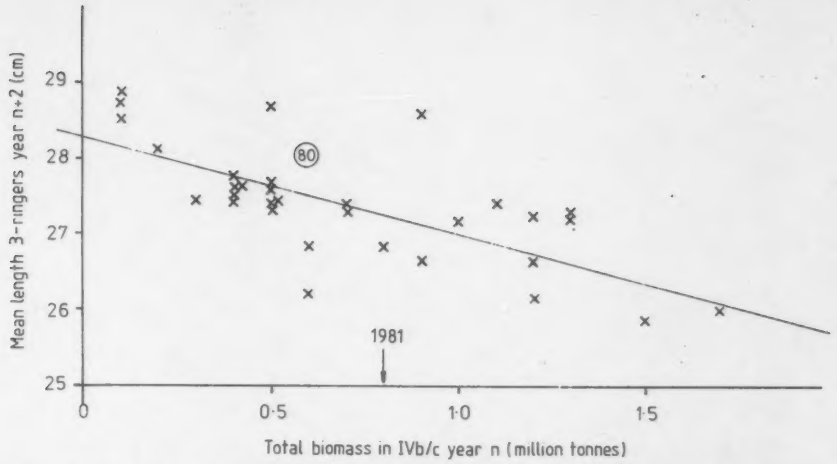

FIG. 13. Correlation of mean length of Bank 3-ringers in year $n + 2$ with biomass on 1 January in year n. Mean length of 1980 year class indicated as circled point.

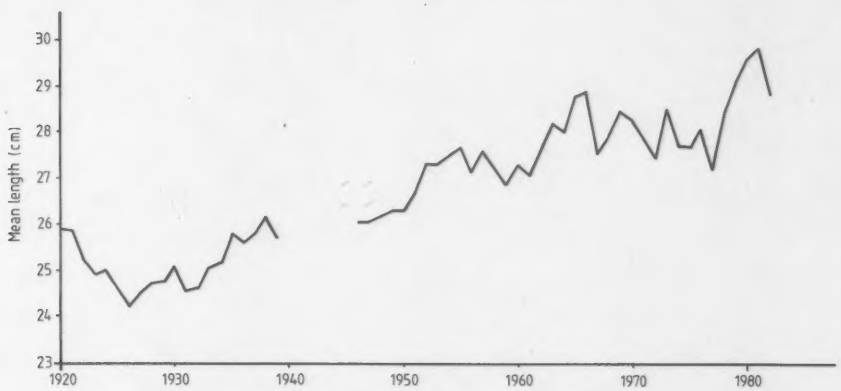

FIG. 14. Mean lengths of Downs 4-ringers, 1920–82.

is not possible under competitive conditions ..." (Iles 1971, p. 411).

J. M. Last (pers. comm.) recorded in coastal waters heavy predation on sprat post-larvae by herring of 9 cm and upwards. It is easy to conceive that post-larval herring would also be taken if available. Because of the differences in spawning time and their subsequent arrival in the nursery areas, intraspecific competition is not unlikely. Of the total growth increment to the time of first spawning about 60% is laid down as 1-group growth. The young herring, then offshore, would compete not only among themselves but also with the voracious recovering spent adult Bank and Downs fish.

In examining a possible link between growth and herring biomass it would be logical to select the biomass in the area and time when the herring were putting on their major growth increment. In Fig. 13 the mean length of each year class of 3-ringed herring has been correlated with the total biomass of Bank and Downs herring on 1 January in the year they were 1-ringers. Year classes are indicated, and it can be seen that with the increased spawning stock biomasses of recent years, reduction in mean length has occurred.

The Bank herring recovery commenced with the sharp increase in recruitment of the 1979 year class. This year class was produced from a low stock biomass at a time when no fishing was allowed, particularly on the spawning grounds. The period of recovery was monitored in the acoustic survey, and it is of note that when the 1979 year class spawned for the first time this took place within the area used by its progenitors in 1979. With the increase in stock biomass, spawning has spread to grounds occupied in earlier periods, and in some years a second

TABLE 6. Percentage age composition of English northeast coast spawners and acoustic biomass estimates for the Yorkshire coast spawning.

Year	Age (in rings)							Biomass ($t \times 10^{-3}$)
	2	3	4	5	6	7	>8	
1979	12.8	4.3	*40.4*	28.7	2.1	5.3	6.4	12
1980	20.9	9.7	1.4	*53.2*	7.2	0.6	7.0	—
1981	33.4	17.2	13.8	14.0	*17.4*	0.6	3.6	10
1982	*62.2*	18.6	6.9	2.6	1.5	*5.3*	2.9	32
1983	50.9	*33.2*	8.9	3.1	1.2	0.2	0.8	38

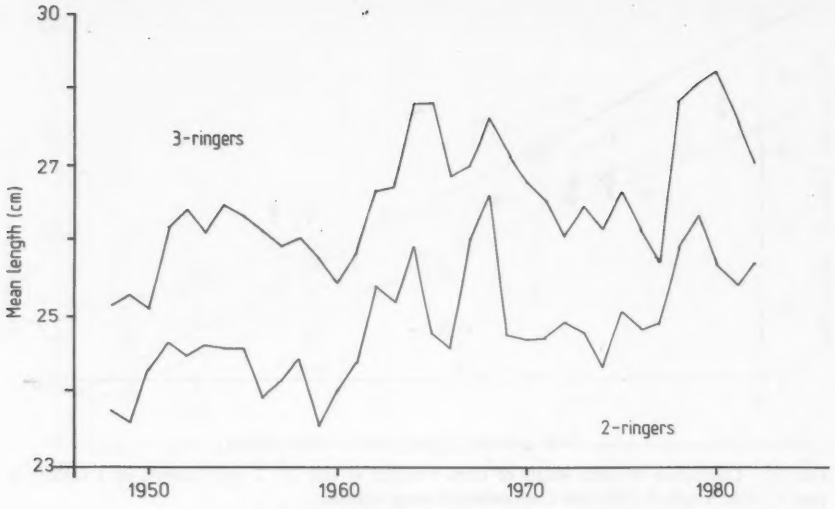

FIG. 15. Mean lengths of Downs 2- and 3-ringers, 1948–82.

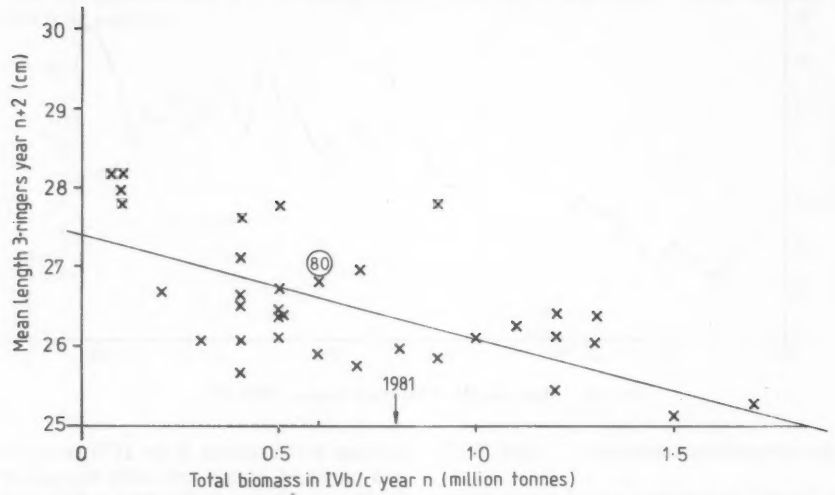

FIG. 16. Correlation of mean lengths of Downs 3-ringers in year $n + 2$ with biomass on 1 January in year n (for 1947–80). Mean length of 1981 year class indicated as circled point.

spawning wave has been recorded on more offshore grounds. As evidenced from the larval production and 0-group data, further increases in recruitment levels are to be expected in 1984 and 1985.

Downs Stock

The Downs spawning stock in 1976 amounted to 3 kt out of a total North Sea spawning stock biomass of 276 kt (Anonymous 1983b). The fishing ban was imposed in 1977. By 1978 the Downs spawning stock biomass had recovered to 26 kt, which generated the large year class responsible for the dramatic recovery of the stock to 150 kt in 1981. The total North Sea spawning stock biomass was estimated at 444 kt (Anonymous 1983b). These stock size estimates are based on the VPA initiated from the English acoustic survey biomass of 1982 (Wood and Johnson 1983b). Larvae abundances recorded in 1981–82 and 1982–83 were of the order of those recorded in 1946–52 (Wood 1980; Bridger 1961).

Under State of the Stocks, Bank Stock, comment was made on the long-term growth change in North Sea herring. The annual mean lengths of 4-ringers for 1919–82 are shown in Fig. 14. The increment ascribed to increased *Calanus* abundance is seen as a plateau in a general increase in length with time. The very high mean lengths over the years 1978–81 correspond with the year classes derived from the period of lowest Downs spawning stock biomasses.

The increment of over 4 cm between 1926 and the 1970s represents an increase in weight at age of about 40%. It is against this background that the magnitude of the post-1947 changes in Downs herring must be viewed (Fig. 15). Again, as

in the Bank stock, the 3-ringed fish are chosen for correlation with the total biomass in the year in which they were 1-group (Fig. 16). As in the Bank herring, there is evidence that a reduction in growth has commenced, and with the increase in stock there is some indication of a return to the historic areas and timings of spawnings.

Conclusions

The resilience of the herring stocks to recover quickly from low biomass levels is an outstanding feature of their recent history. Both Bank and Downs herring have, in 1981 and 1982, returned to spawning biomass levels similar to those of the early 1960s. The recruitment revival has not occurred in the same year class in each area; 1978 spawning season resulted in a high year class in Downs herring, while the 1979 season produced the good Bank recruit year class. The uniform recovery implied in the total North Sea stock management recommendation clearly has not occurred. In view of this, the ICES ACFM was forced to amend its criteria for reopening a fishery.

In May 1980, ACFM noted the possibility of the stock components recovering at different rates (Anonymous 1980). Its criteria for reopening the North Sea fishery required, firstly, that there should be evidence of a recovery of the spawning stock and of improved recruitment and, secondly, that the observed increases in spawning stock and recruitment should be of an order that will ensure that further rebuilding will take place with a limited fishery operating. ACFM considered that these criteria should equally well apply to the individual stocks and proceeded in July 1981 to examine evidence in the three North Sea stocks (Anonymous 1981a). It concluded that a small fishery could be allowed for Downs herring in the winter season 1981–82.

The recommendations for management strategy have thus turned full circle from the attempt made to manage the stocks separately in the mid-1960s, through the total North Sea closure, and back to an attempt at individual stock management. The evidence presented here supports the identity of the Bank and Downs stocks and gives further support to the homing hypothesis.

For management, the prediction of recruitment is very necessary with the present nature of the age composition of the stocks. While the ICES Young Herring Surveys do provide total North Sea stock estimates of juveniles, its original aim of identifying Bank, Downs, and Buchan stocks has still not been achieved. This problem has already been cited by ACFM as a research priority. If, however, Downs year class size is already established at the stages of larvae taken in the surveys as is implied in Fig. 9, then one statistical difficulty in separating the components in the International Young Fish Survey at 1-group is obviated.

However, between the establishment of year class size and recruitment to the adult stock, heavy exploitation may take place. This exploitation takes place in the small-meshed fisheries for raw material fish meal and other animal feeding stuffs. The timing and area of such fisheries will have a different impact on the potential recruitment to the component stocks. There is a marked contrast in recovery rate in IVa spawners compared with the Bank and Downs stocks. Taking the spawning stock biomass in 1977 as unity, the ratios of subsequent annual biomass are given below (Anonymous 1983b):

Spawning stock	Ratio of annual biomass to 1977 biomass				
	1978	1979	1980	1981	1982
IVa	1.20	1.14	1.29	1.38	2.17
Bank	1.14	1.40	1.36	2.43	5.53
Downs	2.89	5.56	6.78	15.56	16.22

These differences, in essence, arise from differences in annual recruitment. A partial explanation could be that the industrial fishery, now tending to work in the northeastern North Sea and in IIIa, would exert higher mortality on the Bank and IVa stock than the Downs herring which are distributed to the south.

The ICES Workshop on Stock Components in Herring Landings from Division IIIa (Anonymous 1983c) showed that the major part of the 0-group catches in July–December and 1-group in January–March were North Sea autumn spawners. ACFM concluded that this might be the main cause of the delayed recovery of recruitment (Anonymous 1983a). They calculated that assuming that Swedish data were applicable to the total catch, then the IIIa fishery in 1978–81 could have reduced the spawning stock in Divisions IVa and IVb combined by about 400 kt.

Maintaining the current partial recovery requires far more direct management action than has been attempted before. It is clear that recruitment is vulnerable, but so are adult herring, particularly at spawning time. Regulations would need to be framed so that each stock may supply its surplus production on a continuing basis. Global measures of TAC limitation would need additional, more detailed specific regulations including marketing aspects and fleet management. Indeed, such a system would require a quantum step in organization and management methods and political cooperation.

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Session 5: Biological, Social, and Economic Aspects of Herring Fisheries Management

Monitoring and Management of the Northeast Atlantic Herring Stocks[1]

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Jakobsson, J. 1985. Monitoring and management of the Northeast Atlantic herring stocks. Can. J. Fish. Aquat. Sci. 42(Supp. 1): 207–221.

The collapse of all the major herring stocks in the Northeast Atlantic in the late 1960s and the early 1970s was undoubtedly the most striking phenomenon in the history of the European fisheries. The events leading to the collapse show similar features for all the herring stocks: a sharp increase in catches over a few years, followed by a rapid decline and a fishing ban. During the period of declining stock abundance, management actions came too late and were not sufficiently restrictive. It appears that managers found it easier to accept a total fishing ban than to agree on severely reduced catches. In many cases it is clear that the fishing ban has been thoroughly enforced, while in other cases illegal fishing has seriously delayed the recovery of the stocks. This has been monitored by various fishery independent methods, such as tagging experiments, trawl surveys, larval surveys, and acoustic surveys. Before advising the reopening of the fishery it has been the general policy of the ICES Advisory Committee for Fishery Management that the spawning stock would be about to reach a minimum target abundance and that there should be firm evidence that recruitment should be on a similar level as it was prior to the collapse. Some stocks are about to or have already fulfilled these criteria, while others are still at a low level and suffering from recruitment failure. When reopening fisheries, setting of total allowable catches (TACs) and national quotas has been universal. Enforcement practices vary greatly within the European countries. In some countries, enforcement of fishing regulations is very strict and carried out on real time bases, while in other countries there appears to be very little enforcement of the existing regulations. Large quantities of herring are sometimes landed and even sold as sprat, whiting, or mackerel. Overshooting TACs is therefore common, and inadequate reporting of catches makes assessment difficult and less reliable than need be. In those cases where fishery regulations are enforced, management is mainly concerned with restricting the activities of the participating vessels so that they do not overfish. In doing so, the best fishing areas have in some cases been closed to fishing, because otherwise the catches would be far too large for the small quantity allocated to each boat. In other cases the catches per boat per night have to be so restricted (because of the large number of participating vessels) that large but unknown quantities of herring are dumped at sea. With the modernized fleets and the large number of boats participating, management has assumed the image of concentrating on "anti-effectiveness." Although the biological management objectives have been well defined and agreed to, the overall management objectives have neither been defined nor agreed to. These must take into account not only the biological objectives but also socioeconomic aspects. A management objective could be to fish the TACs with minimum expense, thus gaining maximum benefit in terms of profits from harvesting the resource. The traditionally free entry and free participation would then be the main obstacle to such an objective. This is especially acute in the case of a schooling species, which can be fished cheaply in large quantities. It is therefore important to develop new methods to restrict effort and investment. This leads to the basic problem of redefining the ownership of the fish stocks. Before an owner is firmly established, management will be under very severe constraints in limiting the entry to the fisheries.

La décimation de tous les grands stocks de hareng de l'Atlantique nord-est vers la fin des années 1960 et au début des années 1970 a été sans contredit le phénomène le plus marquant de l'histoire des pêches européennes. Les événements qui ont mené à cette décimation se ressemblent d'un stock à l'autre : une forte augmentation des prises pendant quelques années, suivie d'un déclin rapide et d'une interdiction de pêcher. Pendant la période de déclin, les mesures gestionnelles ont été prises trop tard et n'étaient pas suffisamment restrictives. Il semble qu'il était plus facile pour les gestionnaires d'accepter une interdiction totale que d'approuver des prises fortement réduites. Dans plusieurs cas, il est clair que l'interdiction de

[1]This paper was presented at the International Symposium on the Biological Characteristics of Herring and Their Implication for Management, convened at Nanaimo, B.C., June 20–22, 1983, commemorating the 75th anniversary of the Pacific Biological Station.

pêcher a été intégralement mise en application tandis que, dans d'autres, la pêche illégale a sérieusement retardé le rétablissement des stocks. C'est ce qu'ont prouvé diverses méthodes indépendantes de contrôle comme des expériences d'étiquetage, des levés au chalut, des études des larves et des levés acoustiques. Avant de conseiller la réouverture de la pêche, le Comité consultatif de gestion des pêches du CIEM exige, comme politique générale, que le stock reproducteur en soit presque à une abondance-cible minimum et qu'il existe des preuves tangibles que le recrutement atteindra un niveau semblable à celui précédant l'effondrement. Certains stocks ont presque ou ont déjà satisfait à ces critères tandis que d'autres restent encore à un faible niveau et souffrent d'un insuccès du recrutement. À la réouverture de la pêche, l'établissement de total de prises allouées (TPA) et de contingents nationaux a été universel. Les méthodes de mise en application varient beaucoup entre les pays européens. Dans certains, l'application des règlements de pêche est très stricte et effectuée sur des bases de temps réel ; chez d'autres, par contre, l'application semble presque inexistante. De grandes quantités de hareng sont parfois débarquées et même vendues comme harenguet, merlan ou maquereau. Le dépassement des TPA est donc chose commune et le compte rendu inadéquat des prises rend l'évaluation difficile et moins fiable qu'il ne le devrait. Dans les cas où les règlements de pêche sont appliqués, la gestion consiste surtout à restreindre les activités des bateaux participants de façon à empêcher la surpêche. Ainsi, les meilleures zones de pêche ont, dans certains cas, été fermées à l'exploitation car, autrement, les prises auraient été trop élevées par rapport aux petites quantités allouées à chaque bateau. Dans d'autres cas, les prises par bateau par nuit doivent être tellement restreintes (à cause du grand nombre de bateaux participants) que de fortes quantités inconnues de hareng sont rejetées la mer. Avec les flotilles modernisées et le nombre élevé de bateaux participants, la gestion donne l'impression de viser l'« anti-efficacité ». Quoique les objectifs gestionnels biologiques aient été bien définis et acceptés, il n'en est pas ainsi pour les objectifs gestionnels globaux. Ces derniers doivent tenir compte non seulement des objectifs biologiques mais aussi des aspects socio-économiques. L'atteinte du TPA avec un minimum de dépenses, ce qui permettrait des avantages maximums en termes de profits générés par l'exploitation de la ressource, pourrait être un objectif gestionnel. L'entrée et la participation traditionnellement libres seraient donc les principaux obstacles à un tel objectif. La difficulté est particulièrement sérieuse dans le cas d'une espèce qui se regroupe en bancs et se prête à une capture en grande quantités, à peu de frais. Il est par conséquent important que de nouvelles méthodes de restriction de l'effort et de l'investissement soient mises au point. Nous revenons au problème fondamental du droit de propriété des stocks de poisson. Avant qu'un propriétaire soit solidement établi, la gestion fera face à de très rigoureuses contraintes pour ce qui est de la restriction de l'accès à la pêche.

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Herring is one of the most common fish species in the Northeast Atlantic Ocean. Consequently, most of the European herring fisheries have a very long history. In some cases it has been shown (Devold 1963; Höglund 1976) that great herring periods alternated with periods when no herring fishing took place. This periodicity is best known for the Atlanto–Scandian herring. In other areas such as the North Sea the herring fisheries appear to have been much more stable, even for several centuries.

The annual yield of the Northeast Atlantic herring fisheries, excluding the Baltic during the period 1950–63, was about 2.5 million t. In the mid-1960s, catches rose to almost 3.5 million t. Then there was a sudden drop to about 1 million t by 1970, which was followed by a continued decline until the late 1970s. In most recent years the yield has been increasing again (Fig. 1). The causes for the collapse of these fisheries were thoroughly analyzed at the sumposium on "The Assessment and Management of Pelagic Fish Stocks," held in Aberdeen in 1978 (Saville 1980). The information presented at that symposium is the basis for this review of the decline of the herring stocks, while the sections on the present state of the stocks are mainly derived from the reports of the Advisory Committee for Fishery Management (ACFM) (Anonymous 1981, 1982, 1983a, 1983b). This committee acts under the auspices of the International Council for the Exploration of the Sea (ICES). The sections on current management practices are based on personal information gathered from my European colleagues.

The present review is not concerned with all herring stocks in the Northeast Atlantic. Notably, a few small stocks near Great Britain and Ireland are omitted, not because they are of no interest but because inclusion of every herring stock in the Northeast Atlantic would diversify the paper to an unacceptable degree. Therefore, only six major herring stocks are dealt with in the following sections.

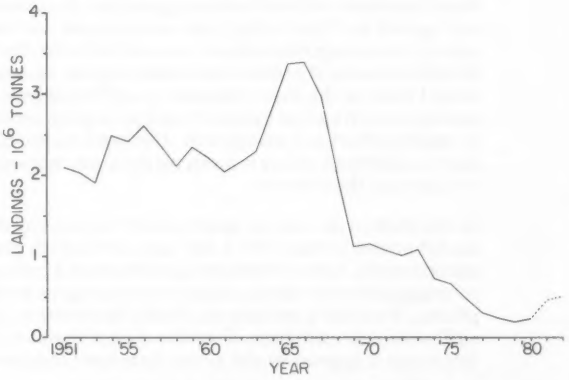

FIG. 1. Landings of herring from the Northeast Atlantic (ICES statistics) excluding catches from the Baltic. Period covered is 1951 to 1982 with the last 2 yr estimated (broken line).

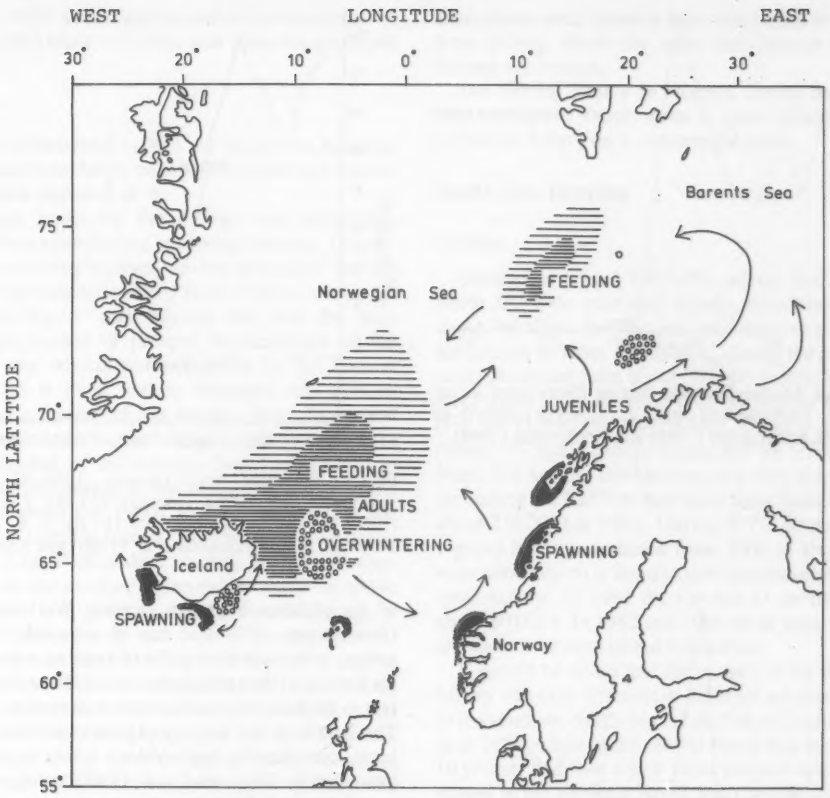

Fig. 2. Migration pattern of the Atlanto–Scandian herring during a period of high stock level (Bakken 1983). Modified from Anonymous (1970b).

Atlanto–Scandian Herring (Norwegian Spring Spawners)

Catches

Traditionally the catches of adult Atlanto–Scandian herring were taken in the Norwegian winter herring fishery, which was mainly based on prespawning concentrations at or near the Norwegian west coast and in the summer herring fishery at Iceland, which was based on feeding concentrations of adult herring. With increased knowledge of the migration pattern (Fig. 2) of this herring stock during the 1950s and in the early 1960s a considerable oceanic fishery developed. During the period 1930–45 the total annual catches of adult herring were about 400 000 t. During the early 1950s the catches increased to 1.4 million t in 1956. Thereafter the catches fell to about 1 million t in 1962 but then increased again to a peak of 1.7 million t in 1966. This was followed by a rapid decline so that in 1968 the catch was only about 270 000 t and in 1970 it had fallen to only 20 000 t (Fig. 3).

In addition to the adult fisheries there was also a juvenile fishery, which mainly consisted of age 0–2 yr herring. This fishery traditionally took place mainly along the coast and in the fjords of northern Norway and to some extent along the Soviet coast in the Barents Sea. During the 1950s, annual catches in this fishery varied between 150 and about 300 000 t but during the last 1960s increased to about 0.5 million t in 1967 and 1968. This fishery continued after the fishing for adult herring had ceased in the early 1970s. While the catch in numbers in the adult fisheries varied during the early 1960s from 1.6×10^9 to about 5.4×10^9 (in 1966), the catches of the juvenile herring varied from about 6×10^9 to about 27×10^9. Therefore, the catch of the juvenile herring far outnumbered the catch of adult herring.

Assessment of the Stock

Traditionally the recruitment to the adult stock was based on few but very strong year classes. Thus, the 1950 and 1959 year classes were strong but all the year classes in between were usually considered weak ones. Dragesund et al. (1980) have, on the other hand, explained that the exploitation rate of young herring was very high during the entire period 1950–69. Thus, the year classes in the 1950s, which have traditionally been described as weak, were all of what could be called normal strength, i.e. 10×10^9 to 30×10^9 fish at the 0-group stage (Fig. 4). However year classes of strength less than 20×10^9 as 0-groups survived the fishery only in small quantities to reach the age of 4 yr. Thus, the year classes 1963, 1964, and 1966, which all were about 20×10^9 in the 0-group stage, were either fished out as 0- and 1-group or as prerecruits somewhat later in their life span.

Dragesund et al. (1980) have estimated the spawning stock size of the Atlanto–Scandian herring during the period 1950–71 using a virtual population analysis (VPA) (Fig. 5). In order to initiate the VPA they assumed a fishing mortality of 0.3 on the

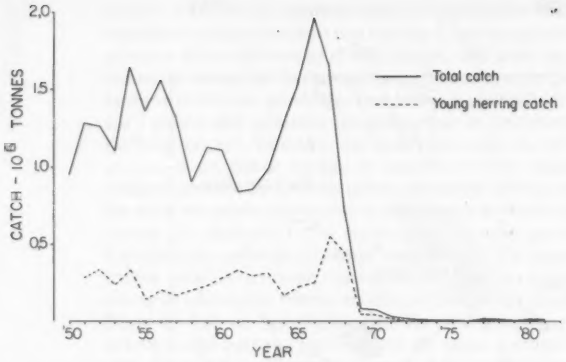

FIG. 3. Landings of Atlanto–Scandian herring (Norwegian spring spawners), 1950–82. Young herring catch i.e. catches of mainly 0- to 2-yr-old herring, from Schumacher (1980) and Anonymous (1984).

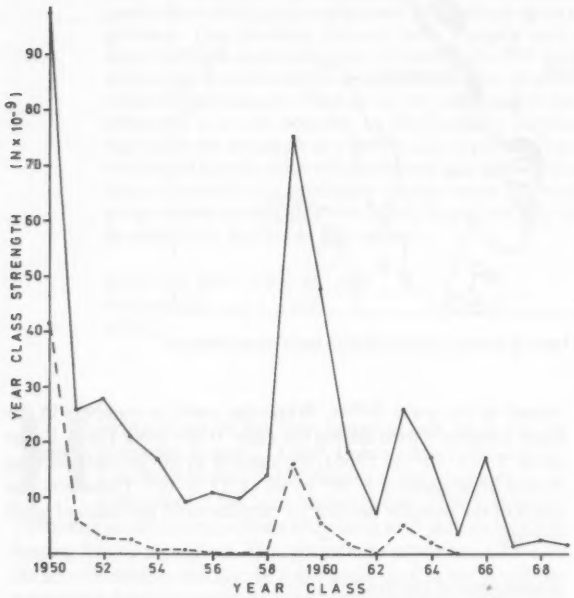

FIG. 4. Year class strength (Norwegian spring spawners) in number as 0-group and 4-yr-olds (broken line) for the 1950–69 year classes. From Dragesund and Ulltang (1978).

year classes that were fully recruited to the spawning stock in 1971 (corresponding to a spawning stock size of about 30 000 t). According to this assessment the spawning stock size was at a level of about 9 million t in 1950 and decreased to about 7 million t in 1953. From 1954 to 1957 the strong 1950 year class gradually recruited to the spawning stock, resulting in an increase in stock size to about 10 million t in 1957. The spawning stock then decreased again as a result of poor recruitment to about 2.5 million t in 1963. From 1963 to 1965 the spawning stock size increased again, reaching about 3.7 million t in 1965. This was due to the recruitment of two strong year classes (1959, 1960). From 1966 to 1969 the spawning stock collapsed due to an almost complete lack of recruitment to the adult stock and rapidly increasing fishing mortalities. Comparing this estimate of stock size with earlier estimates

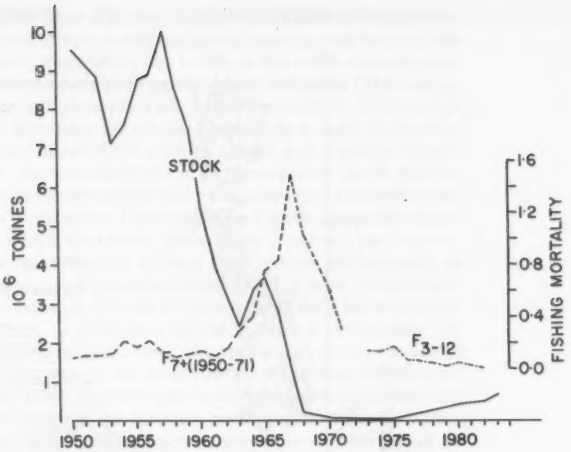

FIG. 5. Spawning stock biomass, 1950–82 (Norwegian spring spawners), and fishing mortality (F) for 7-yr and older herring (1950–70) and fishing mortality (F) for 3- to 12-yr-old herring in 1973–82. From Dragesund et al. (1980) and Anonymous (1984).

of the Atlanto–Scandian Herring Working Group of ICES (Anonymous 1970b) it can be concluded that the working group, using mainly results of tagging experiments, assessed the decline of the stock in the late 1950s and early 1960s more or less in the same way as the latter assessment, referred to above. The results of the tagging experiments indicated, on the other hand, considerably higher stock levels in the mid-1960s than estimated by Dragesund et al. (1980) using a VPA. It should be noted that the VPA assumes a constant natural mortality so that any change in the natural mortality towards the collapse of the stock would invalidate the VPA results at the end of the period in question (Dragesund and Ulltang 1978).

After the collapse of the stock at the beginning of the 1970s a program to monitor the state of the stock was initiated. This included (a) echo surveys on the spawning and feeding grounds, (b) larval surveys, (c) echo abundance surveys of 0-group herring in coastal areas, and (d) tagging experiments. The tagging project was started in 1974 and about 30 000 herring have since been tagged annually. The herring were internally tagged and released at various localities along the Norwegian coast. During each winter 400 to about 1000 t have been caught in experimental fishing on or near the spawning grounds, and between 1 and 2 million herring have been effectively screened for tags in a tag-detector.

Since 1979 the returns from the tagging experiments have been used to calculate the total annual mortality coefficient and the spawning stock abundance of the Norwegian spring spawners. Using the results of the tagging project and the catch in number, the Atlanto–Scandian Herring Working Group calculated fishing mortalities that were used to initiate a VPA. The results of the VPA indicate that the spawning stock increased from 84 000 t in 1973 to about 400 000 t in 1978. During 1979–82, the spawning stock remained at the level of about 400 000–500 000 t (Anonymous 1983a). As pointed out before, the spawning stock biomass of the Norwegian spring spawners was between 5 and 10 million t in the 1950s.

The stock abundance in the early 1980s was 5–10% of its earlier size. Similarly, the recruitment level was only a very small fraction of that observed in earlier periods. With the

recruitment of the 1979 year class the stock size increased to about 650 000 t in 1983 and a very large year class was produced that year.

Management

As pointed out by Sætersdal (1980) the fishery on Atlanto–Scandian herring had completely collapsed without any restriction ever having been imposed on it.

In their thorough paper on the biology and population dynamics of the Norwegian spring spawning herring, Dragesund et al. (1980) analyzed various "saving strategies" for the stock and came to the conclusion that "In the 1960s a minimum landing size protecting 0- and 1-group fish was the only regulatory measure needed to prevent the depletion of the stock." Although this advice was not given by the Liaison Committee of ICES it must not be forgotten that various scientists realized the severity of this fishery. Thus, Marty and Fedorov (1963) concluded: "the first thing to do in attempting to ratonalize the utilization of the Atlanto–Scandian stock is to consider the problem of putting an end to the mass catch of the young fish." Throughout the 1960s and the early 1970s the effect of the 0- and 1-group fishery was the subject of heavy debate within the Atlanto–Scandian Herring Working Group. The main reason why the working group did not reach the above conclusion was that it was given data that indicated that major parts of the nursery areas for 0- and 1-group herring were far offshore and entirely outside the fishing area of the Norwegian 0- and 1-group fishery. When the scientists concerned at long last agreed to give this advice in 1970 it is of interest to note that even at this late date the coastal state was not able to accept a minimum landing size for the Norwegian spring-spawning herring (Anonymous 1970a). Fishing for adult herring had ceased 2 yr earlier.

The use of herring for reduction purposes was prohibited in Norway from January 1971. This was probably the first practical management action to protect the Atlanto–Scandian herring (Norwegian spring spawners). This regulation prevented the complete extinction of the 1969 year class, which had been subjected to heavy fishing as 0- and 1-group. This is of particular interest because the present stock of Norwegian spring spawners are practically all descendants of this year class, which spawned for the first time in 1972 and 1973. During the period 1972–75 the herring fishery was limited by trilateral agreements between Norway, USSR, and Iceland. The catches (all taken by Norway) decreased to about 3000 t in 1975. In 1976 the advice given by ICES to cease commercial fishing was accepted. In 1978 the fishery was reopened with a national quota for Norway of 7500 t. Reported catches were 9800 t whereas the total catches included unreported catches are estimated to be about twice that amount. In 1979 the fishery was closed again apart from some experimental fishing for the recovery of tags.

During the period 1980–83 the national quota for Norway was gradually increased from 930 to about 20 000 t. These quotas have been divided between 450–560 ringnetters and about 2500 boats fishing with gill nets.

It goes without saying that the division of such a small national quota between several thousand fishermen must be a very difficult task. In selecting the ringnetters it has been a prerequisite that they have in earlier years participated in the traditional herring fisheries before the collapse of the stock. Similarly, it must be very difficult to enforce the fishery regulations when about 3000 boats are involved. In order to avoid large catches, which would be in excess of the small allocations, area closures have been used to prevent the boats from fishing where the main and densest concentrations of herring are located.

The herring fishery in Norway during the period 1980–83 thus resembled much more a sport fishery than a real and profitable fishery on a commercial scale.

North Sea Herring

Catches

During the period 1947–63, annual herring catches in the North Sea were relatively steady, fluctuating from 500 000 to about 700 000 t. In 1964 and 1965 there was a sharp increase in the catches to about 1 200 000 t. During the period 1968–72 the catch decreased from about 700 000 to 500 000 t, but thereafter there was a sharp decrease until the fishery was closed in 1977 (Fig. 6). During the 20-yr period 1955–75 the juvenile herring fishery (0- and 1-group) accounted for 50 000–100 000 t. The North Sea herring catches were at a very low level in 1977–79, but during the last 3 yr they have risen from 61 000 t in 1980 to about 235 000 t in 1982. During 1977–80 the catches of 0- and 1-group herring increased from 7000 to about 16 000 t. These were probably to a large extent unavoidable by-catches in the sprat fishery. In 1981 the catches of juvenile herring rose to about 80 000 t. In 1982 and 1983 these were 150 000–160 000 t and cannot be considered by-catches.

It should be noted that the pattern of the development of the fishery was very different in different subareas of the North Sea. In the southern North Sea the decline of landings started as early as in 1954, while in the central North Sea this took place almost 10 yr later and then a few years elapsed again until the decline started in the northern North Sea (Saville and Bailey 1980).

Assessment of the North Sea Herring

There are three main components of the North Sea herring, namely, the Downs herring spawning in the southern North Sea and the English channel, the Bank or central North Sea herring in the central North Sea, and the Orkney–Shetland herring spawning in that area. During the 1950s and 1960s each stock component was studied independently. It was mainly due to the difficulties in allocating catches to the respective components that the Herring Assessment Working Group decided in the early 1970s to assess the North Sea stock as a unit. Based on VPA the total North Sea herring stock was at a high level of 1.5–3 million t during the 1950s to the mid-1960s. There was a sharp decline of the stock during the late 1960s and a further but slower decline until the closing of the fishery in 1977. Although one would conclude from this that the decline of the North Sea herring did not start until the late 1960s, some authors (e.g. Cushing and Burd 1957; Cushing 1959; Burd 1978) have shown that the decline of the Downs stock started much earlier, probably in the mid-1950s.

During the early 1970s the Herring Assessment Working Group was able to monitor the decline in the stock fairly accurately by using fishery data and VPA. The assessment was greatly aided by information on recruitment derived from the International Young Herring Surveys organized by ICES. These give an index of the abundance of 1-ringers in the North Sea (Anonymous 1978a).

As shown in Fig. 7, the fishing mortality on 2-ringers and older herring rose to about 0.7 in 1965 and remained at that level until 1967. During the period 1968–76 the fishing mortality was

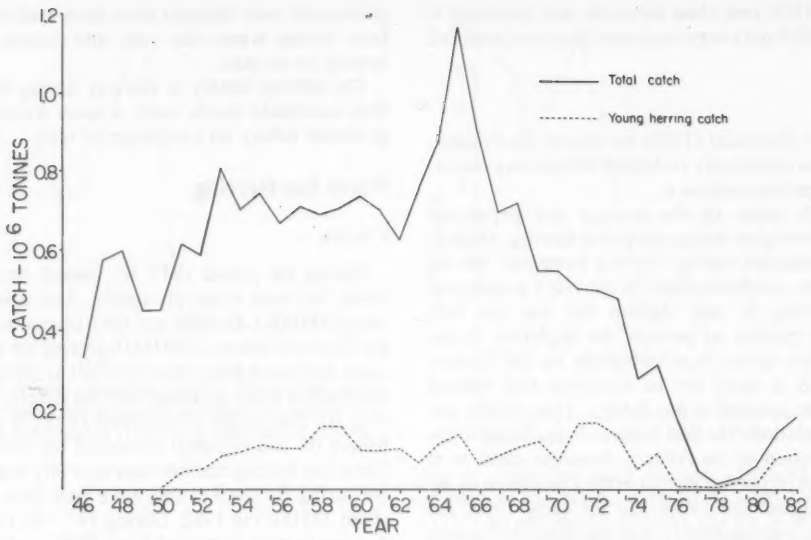

FIG. 6. Catches of North Sea herring for 1946–82. From Schumacher (1980) and Anonymous (1983c).

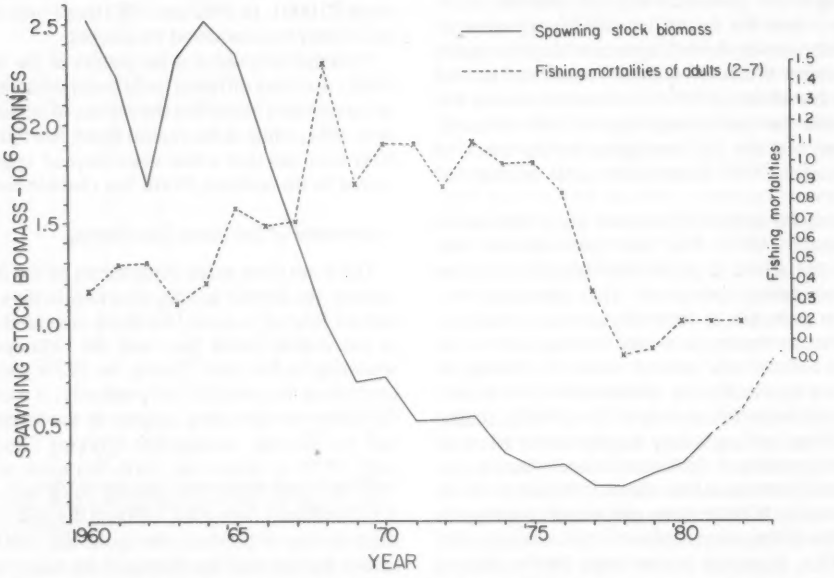

FIG. 7. Spawning stock biomass and fishing mortality rates (F) of adult North Sea herring. From Anonymous (1983c).

about 1.0. With the closing of the fishery in 1977 the fishing mortality fell to a very low level but during the last 3 yr it has been about 0.2.

After the closing of the fishery in 1977 the assessment of the North Sea herring had to be based on fishery independent data. These data have been derived from the international young fish surveys in the North Sea and from the international larval surveys. Thus, by regressing VPA estimates of year class strength against the international young fish survey index for the same year classes during the periods 1958–59 and 1968–74 the current year class strength is predicted. The results of these investigations suggested that the recruitment during the period 1974–79 was at a very low level but the 1980–82 year classes appear to be strong. It should be noted that the long-time (1951–70) average year class strength as numbers of 0-group for the total North Sea is considered to be about 8×10^9. The 1980 and 1981 year classes appear to be 150–180% of this mean (Anonymous 1983c). Thus, there is evidence that the period of low level recruitment to the North Sea herring is past.

Changes in the spawning stock abundance of the North Sea herring have been monitored in recent years mainly by larval surveys. However, the correlations between the larval index and

the spawning stock biomass is not well established in all areas. Thus, according to the 1983 assessment of the Orkney–Shetland herring (Anonymous 1983c), there is no correlation between the spawning stock biomass and the larval index in that area. In the southern North Sea, larval indices have been so high in the last 2 yr that they lie far outside the range on which the regression is based. As a result of these difficulties, acoustic surveys are playing an increasingly important role in monitoring the state of the North Sea herring. In the Orkney–Shetland area, acoustic surveys have been carried out in August on prespawning concentrations of herring, while in the central North Sea, acoustic surveys have been carried out on herring arriving at the spawning grounds. This requires detailed knowledge of the spawning areas and the spawning time. In the southern North Sea, acoustic surveys have been carried out on both prespawning concentrations and spent herring.Thus, stock abundance estimates derived from acoustic surveys and catch data were used to calculate the fishing mortality in 1982 for all the components of the North Sea herring as well as for the total stock.

Management

It has been pointed out (Burd 1974) that the first management action was taken by the North East Atlantic Fisheries Commission (NEAFC) 15 yr after the need for conservation on the North Sea herring was first discussed. This is of course stated with particular reference to the southern North Sea. If, on the other hand, the North Sea herring is looked upon as one unit, the stock did not begin to decrease seriously until the mid-1960s. The decline of the stock was reasonably well documented and consequently the Liaison Committee of ICES advised in 1970 that it would be necessary to reduce the fishing mortality rate by about 50%. As more evidence of declining stock size became available in the early 1970s the advice of the Liaison Committee became more and more severe, and in 1975 it was advised that herring fishing in the North Sea should cease. By this it was meant that directed fishing for herring should be prohibited and rigid restrictions should be enforced on by-catches in industrial fisheries. NEAFC responded by agreeing to a system of closed seasons in 1971–74. When these closed seasons had been in force for about 2 yr it became clear that they had had very little if any effect on the exploitation rate. In 1974 a TAC of almost 500 000 t was accepted for the period July 1974–June 1975. In retrospect this does not seem very realistic because the catch was only 308 000 t in 1974. Similarly, unrealistically high TACs were negotiated for 1975 and 1976. However, in 1975, NEAFC accepted a ban on fishing herring for reduction purposes. This was probably the only practical management action taken by NEAFC in relation to herring because this, at least temporarily, stopped the directed fishing for 0-group in the North Sea.

Any subsequent action to manage the North Sea herring stock within the NEAFC forum was prevented by developments at the United Nations Law of the Sea Conference and the subsequent extension of limits of fisheries jurisdiction by Norway and the European Economic Community (EEC). In the absence of an international agreement a total ban on directed herring fishing in the North Sea was eventually introduced unilaterally within United Kingdom fishing limits for the months October–December 1976 and again from March 1977. In practice, with the extension of fisheries jurisdiction and with the agreement of Norway and EEC countries in 1977, this meant an almost total ban on herring fishing in the whole of the North Sea from February 1977. The catches decreased from 175 000 t in 1976 to only 11 000 t in 1978. In 1979, considerable illegal fishing started and this was continued in 1980 when the total catch was about 61 000 t.

In early 1981 it had become clear that one of the components of the North Sea herring, i.e. the herring in the southern North Sea (Downs herring), had recovered at a much higher rate than the other two components farther north. As a result it was recommended by ACFM that a limited fishery could be allowed in the southern North Sea within the time period October 1981–March 1982, but the total allowable catch (TAC) should not be more than 20 000 t, and that no herring fishery for 1981 should be allowed in the central and northern North Sea. However, the catches in 1981 were in no relation to the recommended 20 000 t, the actual catches being about 141 000 t. It was quite clear that directed fisheries took place in the areas outside the southern North Sea on both adult and juvenile fish. The directed fishery in the southern North Sea in 1981 was about 42 000 t or twice the recommended TAC.

In 1982 a further rebuilding of the herring stock in the southern North Sea was expected, and a TAC of 60 000 t was recommended. The catch figures suggest that the fishing in that area was about 70 000 t, while the fishing in the total North Sea area was 235 000 t. Therefore, about 165 000 t of herring were caught in areas where no fishing should have taken place. The major part of this illegal fishing was actually on 0- and 1-group herring (Fig. 8). It was illegal because (a) it took place in an area where herring fishing was forbidden, (b) the herring were reduced to meal and oil, and (c) the herring were smaller than 20 cm i.e. the minimum landing size. It is perhaps ironic that despite the uncontrolled and illegal fishing for herring in 1981–83, the spawning stock in 1984 of the total North Sea herring will probably reach the target set by ACFM of 800 000 t. This is due to the recruitment of two strong year classes.

It is concluded that the fishing ban that was in force in 1977–79 helped to reduce the exploitation rate and thus preserve sufficient spawning potential of the North Sea herring to make possible the production of large year classes in 1979–82. It is further concluded that the large-scale fishing of 0- and 1-group herring that took place in the North Sea and in the Skagerak–Kattegat sea areas seriously delayed the recovery of the North Sea herring.

West of Scotland Herring

Catches

The total annual landings of herring from Division VIa were rather stable for the three decades prior to the mid-1960s and averaged about 60 000 t (Fig. 9). From 1965 there was an increase in annual landings to a peak of 250 000 t in 1973. This was followed by sharp decline to less than 50 000 t in 1977. During the period 1978–80 there was a fishing ban, while catches in 1981 and 1982 were about 51 000 and 92 000 t, respectively. It should be noted that in the last 2 yr these catches came from division VIa northern part. The Herring Assessment Working Group treats this major part of Division VIa as a management unit, while the southernmost part is treated with Divisions VIIb and VIIc, i.e. NW Ireland. The fishery in Division VIa can be divided into two main components, namely, the offshore summer and autumn fishery and the winter fishery, which is mainly conducted in the Minches, the channel between the Scottish mainland and the Hebrides.

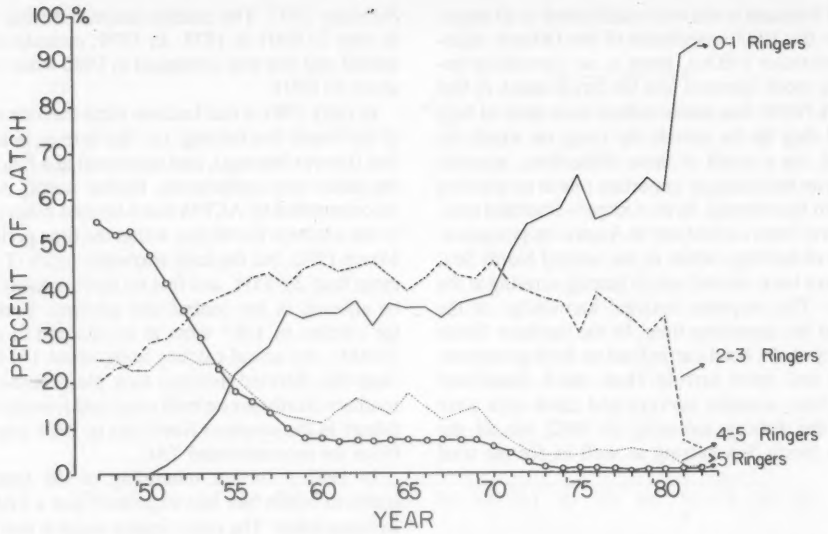

FIG. 8. North Sea herring. Trends in age structure of catches. Moving average over 5 yr plotted at the last year of each period. Redrawn and updated from Schumacher (1980).

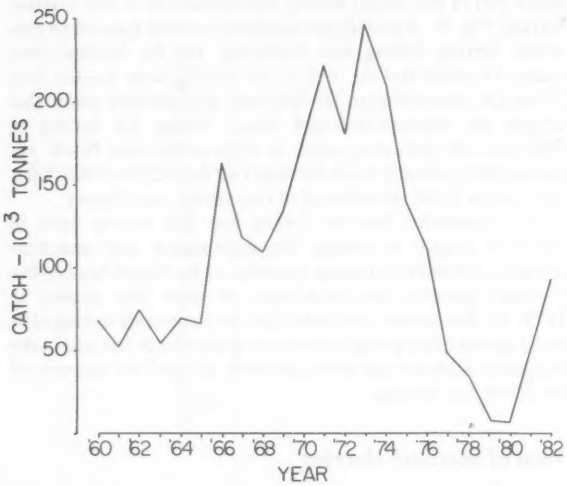

FIG. 9. Catches of herring taken west of Scotland from 1960 to 1982. From Schumacher (1980) and Anonymous (1983c).

Assessment

This herring stock was first considered in 1969 by a herring assessment working group of ICES. The main conclusions of that meeting with respect to VIa herring were that the adult stock could well be around 400 000 t, that the total mortality rate was at a "low level" of 0.4–0.5, and that the stock could support some increased fishing. From 1974 this stock was considered annually by the Herring Assessment Working Group. Prior to that, Saville and Morrison (1973) had given the results of the first VPA carried out on this stock. Except for the 1975 assessment the working group overestimated the stock until 1978 when in retrospect the stock appears to have been more or less accurately estimated. The recruitment to this stock has undergone severe fluctuations. Thus, when the strong 1963 year class was recruited in 1966 the stock abundance almost doubled. During the following period several good year classes were recruited to the stock, culminating in the strong 1969 year class that was recruited in 1972 and brought the stock up to its maximum level of abundance of about 650 000 t (Fig. 10).

During the critical period that followed, there was a drastic reduction in recruitment level. This change was not fully realized at the time. The fishing mortality of the adult herring remained at the relatively low level of about 0.2–0.3 until 1970. Thus, the rapidly increasing catches in the late 1960s did not cause an increase in fishing mortalities due to the high level of recruitment that occurred during that period. The very high fishing mortalities of about 0.8–1.0 were only generated successive to the drastic reduction in recruitment after 1974. It is of interest to compare this development with the North Sea stock, which withstood the high mortalities for a period of about 10 yr before collapsing as compared with only 2 or 3 yr in the west of Scotland herring. Saville and Bailey (1980) suggested that fishing mortality (F) in the western stock was possibly underestimated because it did not account for immigration from the North Sea.

When monitoring the recovery of the stock the herring larval surveys provide the only quantifiable data from which to monitor the changes of the spawning stock in this area. The regressions between larval indices and spawning stock estimates derived from VPA have been used since 1981 to estimate the current spawning stock. According to this stock assessment (Anonymous 1983b) there has been a rapid increase in the spawning stock size from about 70 000 t in 1977 to 380 000 t in 1982.

Management

It has been argued (Sætersdal 1980) that the main reason for inefficient management of the herring stock west of Scotland in the mid-1970s was the inaccuracy of the scientific advice given to managers. However, one must realize that despite these inaccuracies, warnings of general position of the stock and the

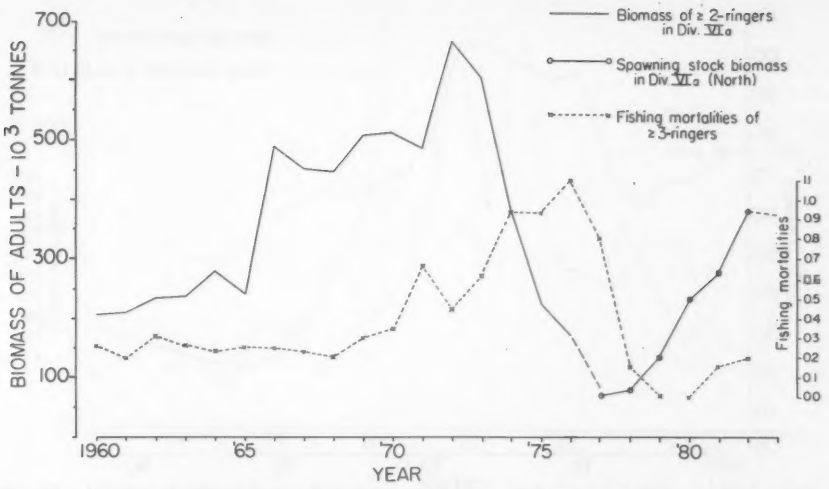

FIG. 10. West of Scotland herring. Spawning stock biomass and fishing mortality rates (F) shown for the years 1960–82. From Saville and Bailey (1980) and Anonymous (1983c).

declining trend at that time were provided. It should be further noted that the managers were unable to agree on TACs even at the optimistic levels of the scientific advice. It is quite clear that they would have been even less able to agree on further reduction in TACs if these had been advised. In all fairness to the scientific community it must be stressed that, at least in 1978, ICES advocated a total fishing ban on this stock. The acceptance and enforcement of this advice in 1978–80 halted the decline of the stock, and with the combined effect of this conservation and improved recruitment, the recovery of stock was almost immediate. In the management of this stock, both during the early 1970s and in the beginning of the 1980s, the main emphasis by the fisheries regulatory body has been on TAC restrictions. National quotas are allocated to individual vessels or companies, and in some cases daily or weekly catch limitations are enforced to help the market cope with the landings.

However, enforcement of quotas varied greatly between countries. For instance, in 1982, one country caught about 4 times its national quota, as suggested by the EEC commission. Additional measures that have been introduced for this stock are a minimum landing size of 20 cm and seasonal closure of the spawning grounds in the northern part of VIa during the spawning season.

Herring at the South Coast of Ireland (Celtic Sea and Division VIIj Herring)

Catches

The development of the catches in this area during the last quarter of a century can be divided into four periods. During 1958–64, average annual catches were less than 20 000 t whereas during the period 1965–69, there was a rapid increase in catches, which averaged about 30 000 t for that period. In 1970–76, catches rapidly declined from about 30 000 t to about 10 000 t. The catches rose again to about 17 000 t in 1981 but in 1982 they were about 13 000 t (Fig. 11).

Assessment

The history of the assessment of the Celtic Sea herring stock

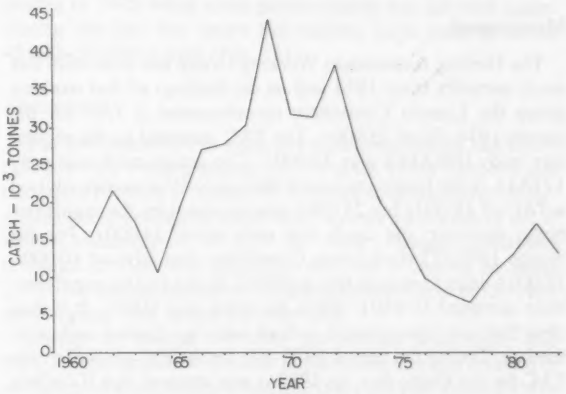

FIG. 11. Catches of Celtic Sea herring from 1960 to 1982. From Schumacher (1980) and Anonymous (1983c).

was thoroughly discussed by Molloy (1980). In the late 1960s there was an increase in the recruitment to the stock, and therefore the biomass of the Celtic Sea herring increased to almost 100 000 t at the end of the 1960s. This attracted increased fishing effort and subsequently, during the early 1970s, there was a rapid decline of the stock accelerated by a complete change in the recruitment level. Until 1982, assessment had been done on the so-called Celtic Sea herring alone but during the last 2 yr the assessment has been done on the combined stocks in the Celtic Sea and in ICES Division VIIj. This new assessment shows the same general picture as the separate assessment of the Celtic Sea. The stock declined to about 20 000 t in 1976 and there was a recovery to about 44 000 t in 1983. The fishing mortalities were about 0.3–0.4 up to about 1968; thereafter there was a rapid increase in fishing mortalities to about 0.7 in the early 1970s. In recent years the fishing mortalities have been fluctuating between 0.4 and 0.6 (Fig. 12). Based on past experience the present management objective of ACFM seems to be that the yield should not be allowed to go beyond 20% of the spawning stock biomass.

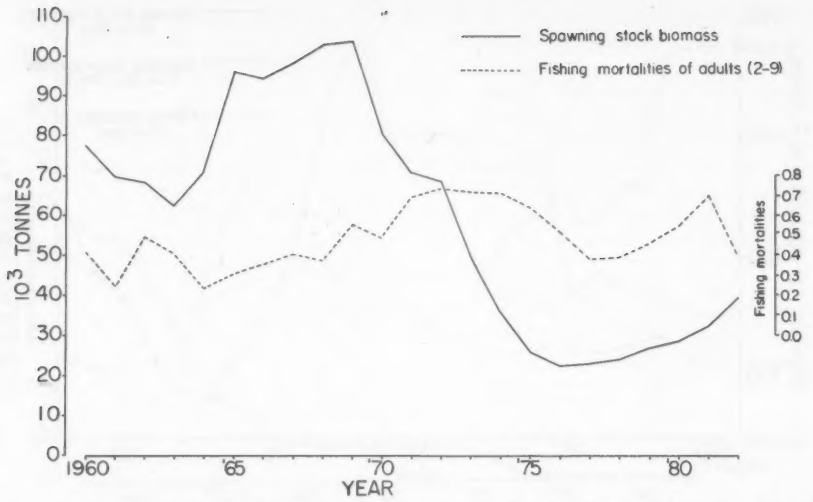

FIG. 12. Spawning stock biomass and fishing mortality rate (F) of adult Celtic Sea herring shown for 1960–82. From Molloy (1980) and Anonymous (1983c).

Management

The Herring Assessment Working Group has dealt with this stock annually since 1974 and on the findings of that working group the Liaison Committee recommended a TAC for the season 1974–75 of 25 000 t. The TAC accepted by the regulatory body (NEAFC) was 32 000 t. The actual catch was only 17 684 t. In the following season the Liaison Committee advised a TAC of 19 000 t but 25 000 t was accepted by the regulatory body; however, the catch was only about 14 000 t. For the season 1976–77 the Liaison Committee first advised 10 000–12 000 t, later to change this to 6500 t. In the end the regulatory body accepted 10 850 t, while the catch was 6000 t. It is thus clear that any management actions were too limited and came too late. During the period 1978–81, the ACFM advised a zero TAC for the Celtic Sea. In 1982 it was stressed that if catches were taken they should be less than 5000 t for the combined areas. Despite the fact that the advice of a fishing ban was accepted by the managers, considerable catches were taken throughout this period. It is quite clear that these illegal catches were large enough to seriously delay the rebuilding of the stock. This is borne out by the relatively high level of fishing mortalities during the ban period 1978–82. Clearly the fishing ban has, therefore, not been enforced. In fact, the only restriction in this fishery has been market capacity. Thus, each boat or pair of boats is subjected to a nightly quota, which is dependent on the size or horsepower of the boats. These nightly quotas have had the drawback that herring is often dumped at sea. In addition, it has to be mentioned, as an extreme example of how completely management has failed, that fishermen have received considerable prices for unmarketable herring in the smaller size categories. These catches were dumped back into the sea at a time when the stock was still at a very low level of abundance compared with earlier periods.

Herring in Skagerak and Kattegat (Division IIIa)

During the post-war period before 1960, catches in this area were about 80 000–100 000 t. The catches increased rapidly during the early 1960s because in that period the North Sea herring stock overwintered in the Skagerak and intensive winter fishery developed there.

During the last 8–10 yr catches in this area have again been in the neighbourhood of 100 000 t showing some tendency of increasing in the last two years (Fig. 13). For many years the sampling of these catches was at a very low level and still is, but since 1974 the Herring Assessment Working Group has for most years been able to estimate the age composition. A very large proportion of these catches is 0- and 1-group herring. Thus, the proportion of the juvenile herring is up to 70% by weight whereas by number the juvenile herring are usually about 90%. Since this has been going on for years and catches have not decreased, the fishery in this area has been a puzzle to herring biologists for some time. However, it is becoming progressively clearer that the majority of the 0- and 1-group herring belong to the North Sea stock, while the majority of the older herring belong to the spring spawning herring in the southwestern Baltic (Rügan herring). These migrate into the Kattegat and Skagerak for feeding during the second half of the year. It is probable that the intensive fishery for 0- and 1-group herring in this area has been one of the main reasons for the delayed recovery of the herring stocks in the northern and central North Sea (Anonymous 1983a).

Despite a large number of recommendations from the Liaison Committee and later from the ACFM, the fishery in this area appears to be completely without control. Even when some of the recommendations for improving, for example the exploitation pattern, have been accepted by the countries concerned, none of these have been enforced. It is of course quite clear that a fishery of this kind could not be continued without management of the stocks migrating through the area, that is the stocks that supply the Skagerak and Kattegat with herring during certain periods of their lifetime or certain times of the year.

Icelandic Spring Spawners

Catches

The annual catches of the Icelandic spring spawners were at a very low level during the early 1950s. This stock spawned at the

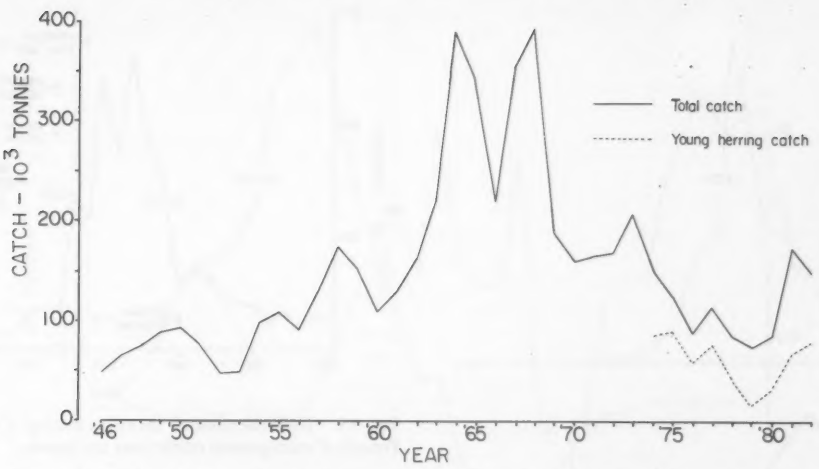

FIG. 13. Catches of Skagerak and Kattegat herring. From Schumacher (1980) and Anonymous (1983c).

south coast of Iceland in March and migrated for feeding purposes to the north coast in summer. With the introduction of sonar and powerblock purse-seining in the late 1950s, catches rose very sharply with a peak of about 280 000 t in 1962. Thereafter there was an equally rapid decline in the catches until the almost total depletion of the stock by 1968 (Fig. 14).

Assessment

During the 1950s the stock was exploited at a very low fishing mortality and the spawning stock biomass increased rapidly due to good recruitment until the late 1960s. At that time there was a rapid increase in the fishing mortality as well as a complete change in recruitment. This caused a rapid decline of the stock, which collapsed completely before management really started. The change in the recruitment coincided with a sharp decline in the level of primary production in Icelandic waters (Thordardóttir 1977) and the resulting low zooplankton production (Asthórsson et al. 1983). This drastic change in the environment almost certainly contributed to the sharp reduction in recruitment during the late 1960s. It is of course difficult to distinguish between environmental and stock abundance effect on the recruitment because after the stock fell below 200 000 t in 1963 the relationship between spawning stock and number of recruits became linear. The Icelandic spring spawning herring should probably be considered as a component of the Atlanto–Scandian herring living at the outer limits of their distribution (Jakobsson 1980). Normally this component is relatively small but it can reach appreciable abundance during periods of favourable environmental regime in Icelandic waters.

Icelandic Summer Spawners

Catches

The annual catches of the summer spawning herring in the post-war period prior to 1960 were generally between 20 000 and 30 000 t. With the introduction of sonar fishing and the powerblock the catches rose rapidly during the early 1960s to about 140 000 t in 1963. During the late 1960s the catches fell drastically until a ban on purse-seine fishing was introduced in the beginning of 1972. The ban remained in force until the last quarter of 1975 when some purse-seining was allowed again. During the last few years the catches have risen to about 45 000–50 000 t a year (Fig. 15).

Assessment

The assessment of this stock has been described by Jakobsson (1980, 1982). Fishing mortalities (F) in the 1950s were low and fluctuated between 0.1 and 0.2. With the introduction of sonar-guided purse-seining in 1960 there was an escalation of the F values, reaching $F = 1.17$ in 1965. Fishing mortalities remained at about this high level until 1971. During the years 1972–74, fishing mortalities were negligible. From 1975–1982 the F values were about 0.2 (Fig. 16).

During the period 1954–63 recruitment was stable and high. This coincided with a low exploitation rate and resulted in an increased stock size to about 300 000 t in 1960. From 1964 to 1970, recruitment was at a very low level. This combined with very high level of F, resulted in the depletion of the stock. The recovery of the stock was relatively rapid because very small spawning stock produced strong year classes in 1971 and 1974.

During the early 1960s, stock sizes and total mortality rates were calculated from tagging data. These calculations indicated a rapid decrease in abundance of the two Icelandic stocks (Jakobsson 1967; Anonymous 1970b). Comparing these calculations with the more recent results from VPA, one sees that there is good agreement between the two entirely different methods until 1965, while a considerable difference exists in 1966, the tagging data indicating a higher stock than VPA.

Since 1973 the recovery of the stock has been monitored by acoustic surveys (Jakobsson 1982). The abundance estimates derived from acoustic surveys for 4-yr-old herring and older appear to be closely correlated with the results of the VPA calculations. This 1:1 correlation provides valuable verification of the absolute value of the acoustic survey estimates.

Management

In 1965 there was a change in the exploitation pattern of the Icelandic herring when a fishery on 1- and 2-group fish developed. In order to prevent an escalation in fishing for juveniles it was advised that a minimum landing size of 25 cm

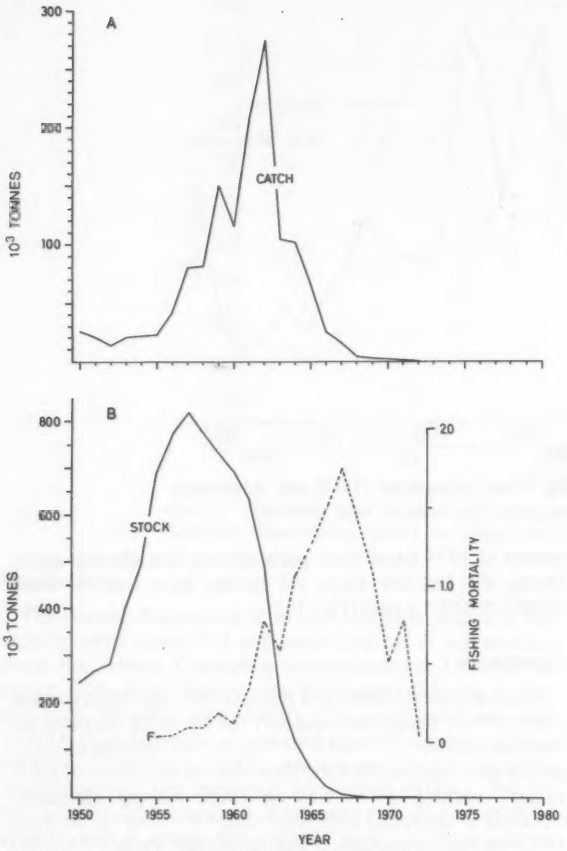

FIG. 14. Icelandic spring-spawning herring. (A) Annual catch, 1950–71, and (B)spawning biomass and fishing mortality (F) for 4-yr and older herring.

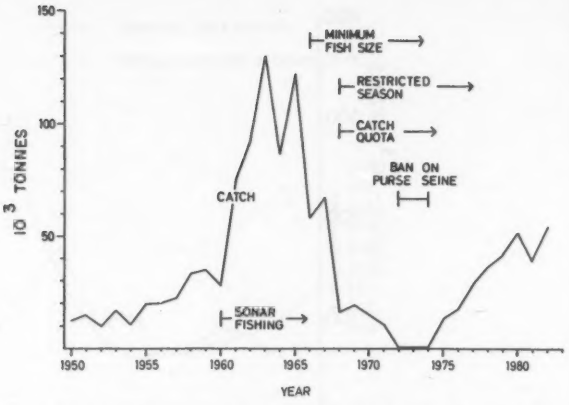

FIG. 15. Icelandic summer spawning herring. Catches for 1950–82. Periods of management restrictions are shown.

should be adopted in 1966. The Icelandic government accepted a minimum landing size of 23 cm. This was too low to prevent or even reduce the fishing of 2-ringers but prevented any fishing of 1-ringers. In early 1967 it was again advised that the minimum landing size be increased to 25 cm, that a TAC for the Icelandic herring be set, and that a closed season be enforced from March 1 to May 15. This advice was ignored in 1967 with the exception of the closed season. Without any TAC there was a sharp increase in fishing mortality of all exploited age groups of both stocks in 1967. In 1968 the minimum landing size was increased to 25 cm, the TAC advised for 1967 was set for 1968, and a closed season was enforced from March 1 to August 15. Unfortunately, these management actions came too late and were not severe enough to have any effect. In 1969–71 the closed season covered the period February 1–September 1 and a precautionary TAC of 25 000 t was set. This was never reached, however, and by the end of 1971 the government was advised to ban all herring fishing except drift-netting. This was accepted and the ban enforced from February 1, 1972. This was almost equivalent to a total ban because drift-netting had not been practised by Iceland since 1960 and very few boats had any gear of this type. During the 8 yr since the reopening of the fishery in 1975 it was managed through TACs and individual allocations to purse seiners. The TACs have been divided between drift-net boats (which usually have been allocated 30–40% of the total) and purse seiners. The fishery takes place in the autumn when the herring are in prime condition. In the most recent years a ceiling has been put on individual drift-net catches but otherwise the drifters have been allowed to fish as much as they can until their total quota has been filled. The purse-seine quota has been allocated equally to the participating boats. In 1982 about 150 purse seiners applied for participation in the fishery, but according to an agreement with the vessel owners as well as the trade unions only half of these boats were allowed to fish in 1982 on the understanding that the other half would be allowed to fish in 1983.

In addition to the quota regulations, a minimum landing size of 27 cm is in force and there is a closed season for about 9 mo each year. In order to enforce the various regulations, several inspectors are placed on board the herring boats and in the harbours where the catch is landed. If the fleet starts fishing where there are excessive numbers of undersized fish this is immediately reported to the Marine Research Institute, which has, for this reason, the legislative power to close any area to fishing. The procedure of closing a given fishing area only takes 1 or 2 h. Any excessive catches are confiscated immediately.

Discussion

The collapse of all the major herring stocks in the Northeast Atlantic during the late 1960s and the early 1970s was undoubtedly one of the most striking events in the history of the European fisheries that has ever occurred. When the scientific community started to discuss overfishing in the 1930s and subsequent years, this discussion was aimed at demersal species. The herring stocks being nearer the origin of the food chain were considered to be of such abundance that fishing would have very little effect on them.

In those early years much of the discussion about assessment and management of fish stocks centred about the yield curve. Unlike some demersal species the herring yield curves do not normally have a defined maximum on them. Therefore, one could not use the argument that by reducing fishing to F_{max} one would increase the yield per recruit in the herring fisheries. In those days, concern for the spawning stock was leered at, to say the least, because stock–recruitment relationships were difficult to prove while stocks were not yet depleted. When individual

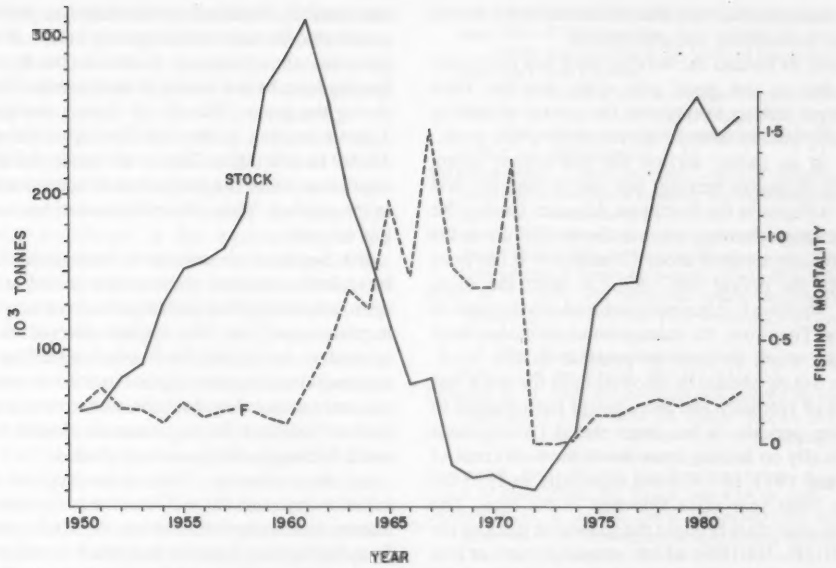

FIG. 16. Spawning stock biomass (Icelandic summer spawners) and fishing mortality rate (F) for 3-yr and older herring, 1950–82.

scientists tried to prove that the fishing was generating high mortalities, as in the case of the herring in the southern North Sea at the end of the 1950s, this only provoked endless disputes from other scientists who still held the view that fishing hardly ever affected herring stocks.

From bitter experience one has now learned a number of lessons, e.g. that the schooling behaviour of herring makes it possible for a fleet with modern technique to obtain very high catches until the stock is depleted (Ulltang 1980; Pope 1980). Thus, a fishing fleet of a given capacity and with adequate landing facilities will take a constant catch from a rapidly declining stock almost until the last school has been scooped out of the sea. One has also learned that their production capacity is relatively lower for herring than for various demersal species such as cod. This means that a herring stock of a given size is not able to withstand as high a fishing mortality as a cod stock of similar size. It is also possible that at low levels of abundance the schooling mechanism of herring renders them more vulnerable to a stock of predators that may be capable of inflicting an increased level of predation on a depleted herring stock, resulting in a higher natural mortality rate. Thus, for instance, a given stock of killer whales feeding on wintering concentrations of herring will eat a constant quantity each day, regardless of the size of the schools of the winter concentrations, in the same way as a fishing fleet of given size will take a constant catch. This would rapidly increase natural mortality with decreasing stocks.

When the European herring stocks had been depleted, certain criteria were developed that should be met before the fishery should be reopened. In general, there should be firm evidence that the stock was about to recover to former abundance, which in earlier years had been sufficient to keep the stock in normal production. There should also be firm evidence that recruitment had returned to earlier levels.

In order to monitor the recovery of the stocks the scientists had to use fishery independent methods as described in earlier sections. In summary, one can say that for the Norwegian spring spawners (Atlanto–Scandian herring) one uses tagging for monitoring the spawning stock and acoustic surveys for monitoring the recruitment. As regards the Icelandic summer-spawning stock one relies almost entirely on acoustic surveys. For the North Sea herring one has until recently mainly relied on larval abundance surveys for monitoring changes in the spawning stocks, while recruitment has been estimated from bottom trawl surveys of 1-ringers. Larval surveys have been used for the herring west of Scotland and to some extent also for the herring at south Ireland. In the Skagerak and Kattegat area one has resorted to acoustic surveys. In the most recent year or two, acoustic surveys have also played increasingly important roles in the assessment of the North Sea herring.

It is of interest to note that most of these stocks are now fulfilling the criteria for reopening the fishery. Thus, as regards the Icelandic summer spawners, the fishery could be reopened already in 1975 when other fisheries were being closed. The early recovery of this stock was due to the fact that two good year classes (1971 and 1974) were recruited to the stock despite a very small spawning stock. This is ascribed to changes in environmental conditions in Icelandic waters during the early 1970s. The fishing ban from 1971 to 1975 prevented the complete collapse of the stock so that rapid recovery was possible when environmental conditions became favourable.

The North Sea herring will probably have recovered to 800 000 t in 1983 or 1984. It has already produced some strong year classes and will, therefore, have met the criteria put forward by the Advisory Committee for Fishery Management in 1983 or in 1984. This is happening despite the fact that almost uncontrolled and illegal fishing for juvenile herring has taken place during the last 2 yr as well as intensive fishing for juveniles in adjourning fishing areas. However, the fishing ban that was in force in 1977–79 helped to preserve sufficient spawning potential to make possible the production of large year classes that have partially survived the fishing for juveniles and will recruit to the adult stock in 1982–84.

The rapid recovery of the herring stocks west of Scotland is mainly due to the fact that the fishing ban was observed for 2 or

3 yr and that the stock decline was thus halted before a severe stock–recruitment relationship was established.

At the south coast of Ireland the herring stock has recovered to some extent due to one good year class that has been recruited, but illegal fishing throughout the period of fishing ban has undoubtedly greatly delayed the recovery of the stock.

As mentioned in an earlier section the Norwegian spring spawners (Atlanto–Scandian herring) was one of the very first herring stocks to collapse in the Northeast Atlantic. During the 1950s this was the largest herring stock in the area, if not in the world, with a spawning stock of about 10 million t. It has been shown that during the period 1967–82, i.e. after the stock declined below 2.5 million t, it has not produced any average or strong year classes. Therefore, the management advice has been to try to bring the stock as soon as possible to this level. Consequently, no fishing should be allowed until the stock has shown clear signs of recovery and recruitment has returned to the level of earlier periods. It has been stated (Anonymous 1978b) that practically no herring spawned at the west coast of Norway in 1970 and 1971. In 1972 and especially in 1973 the remainder of the 1969 year class spawned in the area. The descendants of this year class brought the spawning stock to the level of about 400 000–500 000 t which remained more or less constant in the period 1980–82. This is only about 5% of the former level of abundance. Similarly, recruiting year classes were only a small fraction of those that were recruited to the stock in earlier periods. The rate of recovery has, therefore, been exceedingly slow and the stock provides us with an example of recruitment failure for about 12 yr. This was brought to an end with the production of the strong 1983 year class.

After the bitter experience in the late 1960s and the early 1970s, herring scientists in Europe now agree that their management advice must take into account the following: (a) herring stocks should be exploited at a relatively low exploitation rate, (b) consideration must be given to the size of the spawning stock and at all events it must be kept above a certain critical level, and (c) there must be effective recruitment studies in order to monitor any failure in recruitment.

In the past, management of herring stocks has failed because one has usually done too little too late. It is clear that improved management of the herring stocks demands a more effective dialogue between the scientists and management bodies and much greater readiness on the part of the latter to react quickly to advice, particularly in situations of adverse and unpredictable changes. Compared with earlier periods this should be more easily done at present because management bodies have changed and should be more effective after the extension of fishery limits to 200 nautical miles. Thus, the Icelandic summer spawners are under the regime of the Icelandic state, and similarly, Norwegian spring spawners are only managed and exploited by Norway. The herring stocks west of Scotland and south of Ireland are managed at the responsibility of the EEC.

With the reopening of the fisheries it is of interest to compare management methods applied by the different management authorities. These include the following:

(a) *Minimum landing size* has been accepted for all these stocks. For the Icelandic summer spawners this is 27 cm. In the case of the Icelandic summer spawners this is enforced on a real time basis, mainly by closing areas when the fishing fleet concentrates on herring schools with an unacceptably high proportion of small herring. In other areas it appears that the enforcement is mainly when the herring is landed. With the acceptance of the NEAFC regulation prohibiting reduction to meal and oil, this minimum landing size problem should not be a severe one because small herring below 20 cm are usually not used for other purposes. However, the by-catches of juvenile herring have been a severe problem in the North Sea, especially during the years 1981–83. In these years the fishing of 0- and 1-group herring in the so-called sprat fishery increased from 78 000 to 160 000 t. This is of course far above any by-catch regulation, since the proportion of herring was often above 90% in the catches. Thus, the enforcement has not been effective in this respect.

(b) *Seasonal closures* have been applied to all these stocks. In Iceland, seasonal closures are aimed at having the fishery open only during that period of the year in which the herring are in prime condition. This applies also for the Norwegian spring spawners. As regards the North Sea herring in 1981 and 1982, seasonal closures were applied in order to ensure that the fishing was only directed against the southernmost component. In the west of Scotland, herring seasonal closure has been applied to avoid fishing on the spawning grounds.

(c) *Area closures* have been applied for the Icelandic summer spawners on real time bases in order to protect the immature and undersized herring. Area closures for the Atlanto–Scandian herring have been applied in order to protect the very dense concentrations of herring that would unavoidably give rise to larger catches than allocated to individual purse seiners. Area closures in the North Sea have been applied to ensure that fishing is not directed towards certain components of the North Sea herring. In the west of Scotland, area closures have again been combined to seasonal closures to avoid fishing on the spawning grounds.

(d) *TACs* have been applied to all these stocks. In Iceland, TACs are first divided between two groups of boats fishing with different gears, and then the purse-seine catch quota is divided equally between the boats participating in that fishery. These individual catch quotas for boats are enforced on real time bases. In Norway the TAC is also divided between different gear categories, and within each category it is divided between boats depending on the number of the crew on each boat. The maximum number of the crew is limited to eight. For the North Sea the TAC is divided into national quotas. In several countries these are divided between either companies or ships. Enforcement varies greatly from one country to another, and even within one country it varies from year to year. Daily or weekly limitations of catches are common. It is concluded that in most European countries it is legally possible to impose almost all kinds of limitations on the fishing fleet although enforcement is not always effective.

(e) *Effort restrictions* have been tried on some of the stocks. In 1982 about 150 purse seiners applied for a licence to fish herring in Iceland. The effort was restricted to 75 boats on the understanding that the other 75 boats would be allowed to fish in 1983. The problem of effort restriction is even greater in Norway than in Iceland. In 1982 a TAC of about 13 000 t was divided in such a way that about 7800 t would be caught by the ring-netters and about 5200 with set-nets. In all, 1151 ring-netters applied, of which 564 vessels were granted licences. In addition there were about 2363 vessels that were granted licences to catch herring with set-nets. This meant that the maximum quota for the ring-netters was about 24 t per vessel. This is of course a very small quota for a ring-netter when it is considered that the catch from one ring-net shot is commonly hundreds of tonnes.

The problems of effort restrictions in other European coun-

tries are probably not as enormous as in Norway. There is, however, no doubt that the existing modern and efficient fleets could fish the TACs allocated to them many times each year. In Norway, there is an extreme case of almost 3000 vessels taking a very small TAC, where only a few vessels are needed.

Traditionally the exploitation of the herring stocks as well as other fish stocks differs from the exploitation of most of the other natural resources in that there has been a free entry into the fishery. By this it is meant that anyone who had the equipment and the boats could participate in the exploitation of the resource. With the application of modern technology in the herring fisheries the system of free entry is responsible for the most irrational competition and expenditure. As pointed out by Højdal (1983), the biological objectives in the management of herring stocks are well formulated. However, these biological objectives are only a part of the overall management objective. This must be a complex of biological and socioeconomic considerations. For instance, is the target in managing herring stocks to catch the TAC at the lowest possible expense in order to maximize profits or is the objective to give the maximum number of people employment in utilizing the resource? If the management objective is the former then the question immediately arises as to who is to be allowed to harvest the resource in this way and who should get the enormous profits. This again leads to the question of ownership. Do the herring stocks belong to the fishermen, the boat owners, those who cure the herring, or do they belong to the coastal state or the respective nations? Despite several meetings between European managers and scientists it appears that the discussion on these urgent basic problems has not even started. The lack of such discussion, let alone decisions, on these fundamental problems is probably the main constraint that prevents rational management of herring stocks. We will never return to the old system of using only a few set-nets and small open boats to catch the herring. Modern technology has come to this industry. It has brought very severe socioeconomic problems that must be tackled and solved before effective and rational management of herring stocks will be achieved.

Acknowledgements

In preparing this review on the management of the Northeast Atlantic herring stocks I was greatly assisted by several European colleagues who kindly supplied information concerning management practice in their own countries. My thanks are also due to Mr. E. Bakken, Norway, for giving me permission to use drawings from his most recent paper on the Atlanto–Scandian herring.

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History of the Herring Fishery and Review of Artificial Propagation Techiques for Herring in Japan[1]

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According to written records, a Japanese herring fishery has been carried out since 1447, but statistical catch data were not recorded until 1870. The Japanese herring fishery has harvested the so-called Hokkaido spring herring, which spawned near the coast of Hokkaido from March to May. In 1897, the landings reached a peak of 975 000 tonnes but the resources were depleted year by year and this stock became extinct in the 1950's. During the 1960's, Japanese fleets were exploiting the herring stocks in the Northwest Pacific. However, since 1970 these fisheries were limited in their operations by the Japan–Soviet Fisheries Committee and eventually ceased in 1976. At the present time, the Japanese catch of herring is at a low level of several thousand tonnes. The Japanese license system was not designed to conserve the resources, and herring studies were weighted to fishing forecasts only. Many Japanese scientists believed that the strength of herring year-classes fluctuated with changes in food conditions in the early larval stages. Based on artificial egg production techniques developed recently in Japan, herring eggs were successfully hatched, and larvae were cultured artificially and raised to 66.3-mm juveniles with a high survival rate.

Selon les données publiées, les Japonais pratiquent la pêche du hareng depuis 1447, mais aucune statistique sur les prises n'a été recueillie avant 1870. Cette pêche visait le hareng du printemps d'Hokkaido, frayant près de la côte de l'île du même nom de mars à mai. En 1897, les débarquements atteignirent un maximum de 975 000 tonnes. Cependant, les ressources ont diminué d'une année à l'autre et le stock a disparu au cours des années 1950. L'exploitation des stocks de hareng du Pacifique nord-ouest a suivi pendant les années 1960. Toutefois, dès 1970, ces opérations ont été limitées par le comité URSS–Japon des pêches pour finalement cesser en 1976. Actuellement, les prises japonaises de hareng n'atteignent que quelques milles tonnes. Le système japonais de délivrance de permis n'a pas été conçu pour la protection des ressources et les études sur le hareng ont été pondérées seulement en fonction des prévisions de prise. Plusieurs scientifiques japonais croyaient que l'abondance des classes d'âge fluctuait selon les variations des conditions alimentaires pendant les premiers stades larvaires. À l'aide de techniques de production artificielle d'œufs, récemment mises au point au Japon, on a réussi à faire éclore des œufs de hareng et à élever les larves jusqu'au stade juvénile (66,3 mm), avec un taux élevé de survie.

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The history of the herring fishery in Japan is largely divided into two periods, namely, the time of coastal fisheries, which centered on Hokkaido spring herring and lasted up to the 1950's, and that of the far seas gillnet fishery in the Northwest Pacific Ocean, which was developed in the 1960's and lasted up to the middle of the 1970's. The current herring fishery in coastal waters of Japan is on a small scale; the annual catch is only a few thousand tonnes. The catch consists chiefly of Sakhalin herring, migrating in offshore waters on the Sea of Okhotsk side of Hokkaido.

The fishery for Hokkaido spring herring was centered mainly on schools of fish that approached the shorelines of Hokkaido to spawn. The mature eggs of fish caught prior to spawning were processed with salt to suit the taste of Japanese consumers who have long favoured this food. Some gutted bodies were partially processed and dried for direct consumption, but most were processed into meal or used as fertilizer.

Today, the herring fishery has declined greatly compared with previous years. Demands for non-food fish have come to be filled by Japanese sardine, catches of which have increased remarkably. However, the demand for herring as food is still in strong demand. Thus, imports of frozen herring rose from 14 000 metric tonnes (t) in 1979 to 60 000 t in 1982, and imports of herring roe have been maintained at a level of 7000 t.

In the history of Hokkaido's spring herring fishery, no management from the point of resource conservation was ever undertaken. From observing the swarms of herring in the sea every spring, it was not imagined that this particular herring stock was threatened with extinction. The main studies on herring in early days were focused on estimating the fishing prospects through age analysis. In the post-war years, the herring fishery was activated for a time, but declines in the catch began to spread gradually from south to north until the latter part

[1]This paper was presented at the International Symposium on the Biological Characteristics of Herring and Their Implication for Management, convened at Nanaimo, B.C., June 20–22, 1983, commemorating the 75th anniversary of the Pacific Biological Station.

of the 1950's, when the Hokkaido spring herring completely disappeared from the coastal waters of Hokkaido. In this whole period of time, studies could not provide any convincing explanation for the stock extinction, nor was any management proposal made to rationally deal with the problem.

The herring resources fished by the Japanese during the 1960's in the Northwest Pacific region were already exploited by the Soviet coastal fishery. At about the same time as Japanese fishing boats began to operate in the northern part of the Sea of Okhotsk, large-scale fishery operations using round-haul nets had already begun by the Soviet fleets. As a result of these activities, exploitation of these resources became the subject of discussion in the Japan–Soviet Fisheries Committee from 1969 onward, and a certain measure of fishery resource management including closed seasons and areas, etc., began to be adopted on the basis of studies made by the Science and Technology Subcommittee. It cannot be said, however, that these measures were always founded on sufficiently scientific grounds. They were greatly affected by the social and economic factors of the fishery in both countries. The establishment of the 200-mile economic zone by the Soviet Union in 1976 completely excluded Japanese fisheries from the said area.

On the other hand, there have been technical developments in Japan in recent years for artificially assisting in egg production and releases, aimed at expanding useful fishery resources by human efforts. The traditional techniques of hatching and releasing salmon have been improved, while techniques for shellfish such as scallops, shrimps, some species of crabs, sea bream, etc., have been developed and put into practical use. On the basis of these technical developments, the experimental production of eggs and release of young herring was successfully carried out for the first time in Japan in 1982. It is well known that fluctuations in stock size depend on year-class strength. If the theory is correct that year-class strength is determined by the natural environment, especially food conditions, in early life stages, artificial management of the environment at this critical period might make it possible to increase the numbers in a year-class. This could possibly be an effective aid for the recovery of local herring stocks that are either declining or facing extinction. It can be said that resource management through catch controls is a passive method, but that such artificial propagation of resources is a positive management method.

In this report, the history of Japan's herring fishery is reviewed and the shortcomings in management thinking regarding the herring fishery are discussed. The opinions of Japanese scientists with respect to the factors determining year-class strength are mentioned. Lastly, results of recently undertaken technical studies on the successful artificial rearing of herring are presented.

History of the Herring Fishery in Japan

Hokkaido Spring Herring

The herring that migrated to the western coast (Japan Sea side) and the northeastern coast (Sea of Okhotsk side) of Hokkaido were called Hokkaido spring herring (Fig. 1). Records indicate that the earliest herring fishery was made by fishermen in 1447, but the first fishery statistics were not produced until 1871. In the early days, the herring fisheries were operated in a primitive manner in the northwestern coastal area of Honshu Island and began to espand toward the western coast

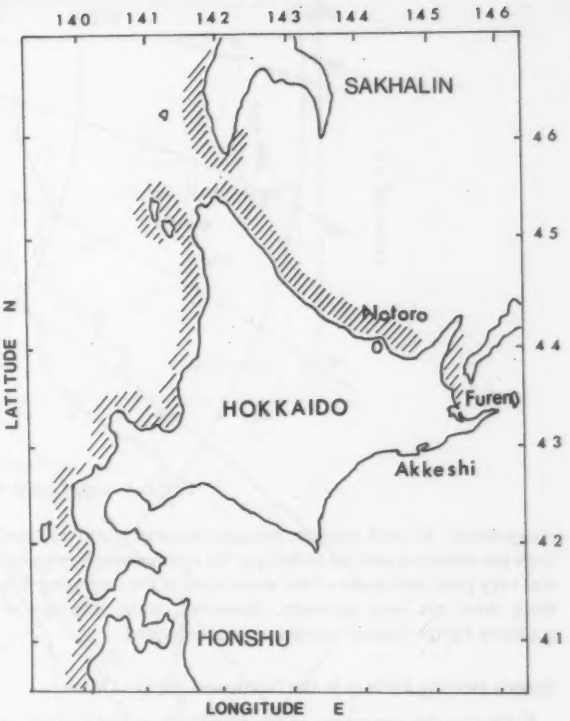

FIG. 1. Spawning grounds of Hokkaido spring herring, off Hokkaido, northern tip of Honshu and southern tip of Sakhalin Islands.

of Hokkaido. In the early part of the nineteenth century, the fishery was extended through the coastal area of the Sea of Okhotsk to the northern part of the east coast of Hokkaido. A stationary trap net fishery was introduced at about this time, and further improvements led to gradual expansion in the catch.

Records for Hokkaido spring herring became available from 1871 (Fig. 2). According to the statistics, the catch showed an increasing trend with some fluctuations and peaked in 1897 at 975 000 t. It is estimated that more than 5000 trap nets were used about that time. From 1898 to 1912 the grounds fished decreased in number from south to north, and the gross catch continued to decline. In 1912 and 1913 a temporary recovery in catch was observed, but thereafter the catch continued to decline. Although there was a slight increase in catch during the Second World War, the Hokkaido spring herring had completely disappeared from the coast of Hokkaido by 1955 (Hanamura 1963; Motoda and Hirano 1963).

There has never been any sufficiently scientific explanation of why the said herring stock, which once produced a catch of close to 1 000 000 t, took the path of decline to its final extinction. One opinion was that variations in population size were caused by anomalous changes in oceanic conditions, as there was an inverse relationship between the variation in seawater temperature and the number of herring, but there was no case study made as the the factors inducing a continuous decline.

In the period of the Hokkaido spring herring fishery, the studies on herring were not directed toward clarifying the cause of fluctuations in population size, but were directed mainly to an estimation of the fishing prospects based on analysis of age

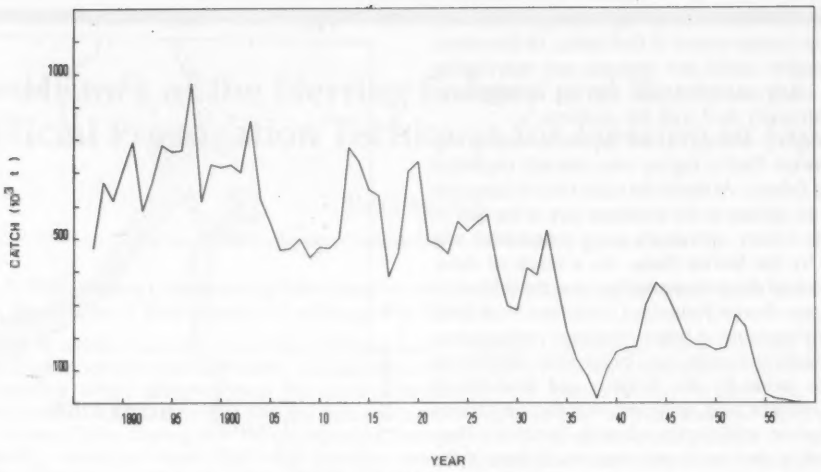

FIG. 2. Annual catch of Hokkaido spring herring.

composition. In such studies, because accurate survival rates were not obtained and the technique for estimating recruitment was very poor, estimates of the abundance of the migrating fish stock were not very accurate. However, some measure of guidance for the fishery operations was provided.

Japan's Herring Fishery in the Northwest Pacific Ocean

Following the extinction of the Hokkaido spring herring, a trawl fishery was initiated in 1955 for Sakhalin herring, which were considered to be a local stock, and a gillnet fishery was operated in the area offshore of Hokkaido in the Sea of Okhotsk. The catches did not exceed the level of several thousand tons and these fisheries did not expand greatly because there was practically no catch of fish suitable for kazunoko (mature fish eggs).

In the early 1960's, Japanese fishing boats discovered the spawning grounds of herring in the northern region of the Okhotsk Sea and at the western end of the Bering Sea and expanded their fishing operations (Fig. 3).

A herring fishery was operated by the Soviet Union for a number of years in the northern region of the Sea of Okhotsk (Fig. 4 and 5). The first Japanese surveys of this herring stock were conducted in 1957. These surveys were conducted from June to October with the use of four research boats for the purpose of determining fishing grounds and conducting biological research and processing experiments, etc. While information regarding the distribution of herring in the region was obtained from the surveys, they were not continued thereafter and thus no adequate information was gained regarding the status of the population.

In June 1965, several fishing boats carried out experimental gillnet operations in the northwestern region of the Sea of Okhotsk. In 1966, a fleet of 66 Japanese vessels sailed north and fished gill nets in Shelehova Bay, northwest of waters of Okhotsk City, and captured ripe herring. Encouraged by the results of these operations, 84 Japanese vessels operated fisheries in the same bay from May to June 1967 and caught 3200 tons of ripe herring. The catch in 1968 dropped sharply. The main fleet of Japanese vessels, thereafter, turned to catching spawning herring in Tauiskaya Bay and gradually expanded their fishing grounds to the western region of the Sea of Okhotsk off Ayan City. From 1969, a driftnet fishery was operated in the western offshore waters of Kamchatka centering on herring in the feeding season in summer and autumn; stable catches were obtained. However, at the 13th Conference of the Japan–Soviet Fisheries Committee (Tokyo, March 1969), the commercial fishery in Shelehova Bay was banned to protect spawning herring. In 1970, at the 14th Conference of the Japan–Soviet Fisheries Committee, a decision was adopted to ban fisheries up to May 15 in waters north of 58°30′ in the Sea of Okhotsk. Thereafter, controls on this fishery were further intensified under strong pressure by the Soviet Union, and at the 15th meeting of the Committee in 1971, fisheries for spawning herring were generally banned except for operations by some survey vessels monitoring the stock. Thus, a commercial fishery for spawning herring by Japanese boats became impossible. The Japanese fishery for feeding herring in the central and eastern region of the Okhotsk continued for a period, but with the establishment of the 200-mile economic zone by the Soviet Union in 1976, this fishery also ended (Kobayashi et al. 1979).

The author would like to note some biological aspects of herring in the Sea of Okhotsk. The herring distributed in Shelehova Bay are called the Gizhiginsk–Kamchatka population. They spawn in Gizhiga Bay. A portion of the population migrates for feeding to waters off the northwest coast of the Kamchatka Peninsula. This group is a relatively small population. On the other hand, the herring that spawn in the coastal areas extending from Tauiskaya Bay to Ayan and migrate to the central part of the Sea of Okhotsk are called the Okhotsk herring and represent the major population in the area.

Herring Fishery in the Western Bering Sea

Distributed in the western Bering Sea are the Korfo–Karaginski herring that spawn in Anapka, Uara, and Korfo bays. These herring have long been exploited by the Soviet fishery. In the 1950's, the Soviet Union began to engage in a purse-seine fishery for these fish. Catch statistics and biological information were gathered in 1960 and thereafter (Kachina and Prohorov 1966).

Japan had conducted fishery explorations since 1958 through a mother-ship type trawl fishery and discovered a promising fishing ground in 1960. In 1961, 23 fleets conducting a gillnet

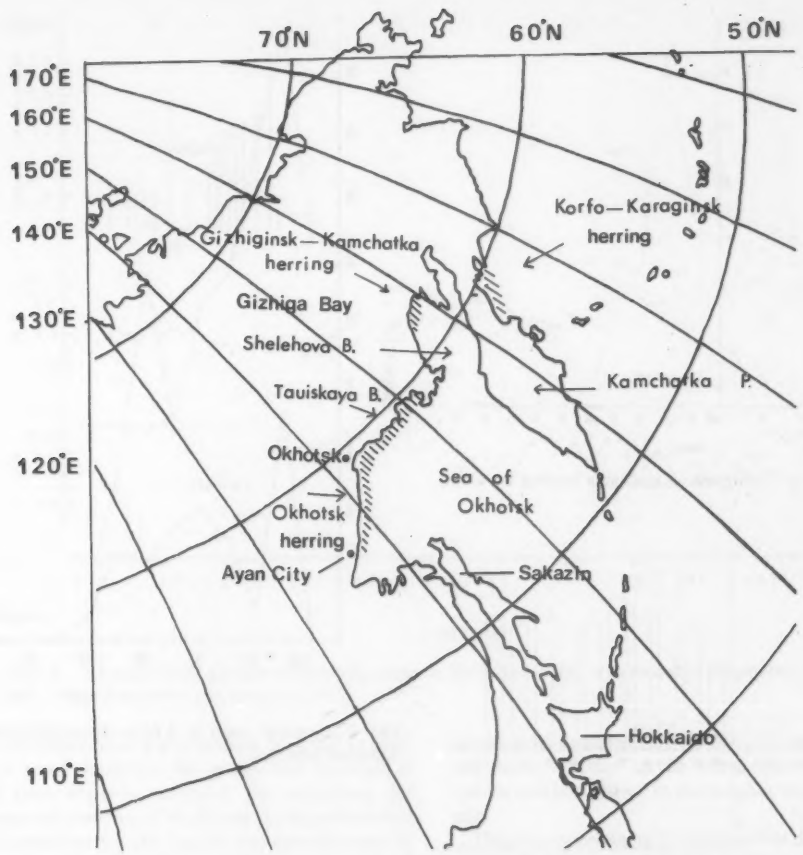

FIG. 3. Spawning grounds of Gizhiginsk–Kamchatka herring, Okhotsk herring, and Korfo–Karaginsh herring.

fishery caught 74 000 tons of herring. However, these operations were not profitable because the price of fish was low at that time and fishery operations were reduced to four to six fleets after 1963. Until 1964, all Japanese fisheries had operated on herring during the feeding season, but in 1965 the fishery also operated on herring migrating for spawning. After 1965, the major fisheries shifted to egg-bearing herring in prespawning stages, which commanded higher prices (Fig. 6). At the 13th meeting of the Japan–Soviet Fisheries Committee, a serious deterioration in the stock level of these herring was discussed, and a decision was adopted to establish a no-fishing area to protect the spawning herring. At the 14th meeting of the Committee held the following year, commercial fishing in the said region was generally banned. Fishery operations by a limited number of research vessels have been carried out since then for the purpose of monitoring the trends in stock size. After 1977, with the establishment of the 200-mile zone, Japanese fisheries, including those by herring research vessels, completely ended (Morita 1983).

License System and Management in Japan

Japan's fisheries are fundamentally based on a license system. The purpose of the system is to coordinate the different types of fisheries as well as to control activities within the same type of fishery so as to avoid conflicts. The system was not designed from the point of view of rational utilization of fishery resources. Generally, the system sets limits to the fishing effort, but the basis of the system is to protect priorities. For this reason, the measures taken by Japan for preservation of the resources were, at the most, limited to closed seasons and partial controls on fishing grounds: a quota system was very seldom introduced.

In the long history of the Hokkaido spring herring fishery, no control measures other than a license system were ever taken in the direction of limiting the catch. In that situation, the emphasis of the studies was placed on forecasting potential catches. No due attention was paid to the relation between the size of the resource and the catch, and it was inevitable that before long a catastrophic situation would develop.

The herring fishery in the Northwest Pacific Ocean was one in which two nations tried to exploit the same resource. In that situation it was possible that international negotiations could have led to certain fishery management measures beyond the traditional systems of each country. However, in the case of herring, the application of the 200-mile limit arrived before the effects of any management measures taken were fully examined.

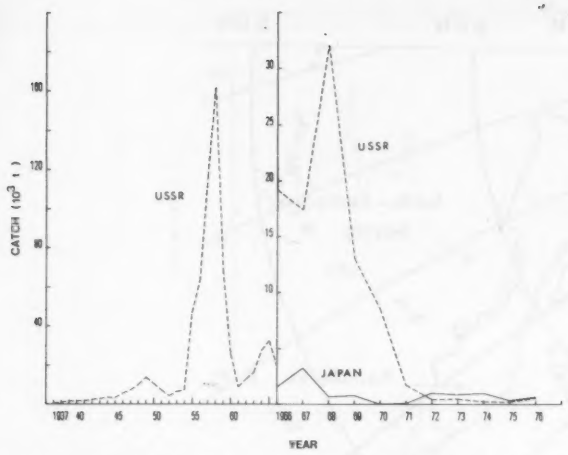

FIG. 4. Annual catch of Gizhiginsk–Kamchatka herring by USSR and Japanese fisheries.

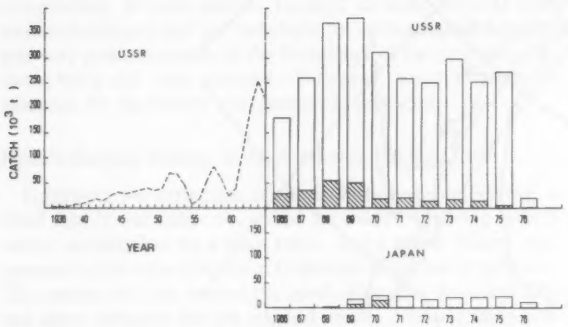

FIG. 5. Annual catch of Okhotsk herring by USSR and Japanese fisheries. The shaded portions indicate spawning herring and the open portions indicate feeding herring.

In view of today's situation, in which fishing ability is sharply increasing while resources are becoming increasingly limited, discussions are under way to seek a system to achieve optimum utilization of resources based on Japan's traditional system.

Factors Determining Year-Class Strength

It is, of course, unreasonable to exert more pressure by catching more of a species whose stock size has deteriorated to the extreme. However, it is not generally considered that there is a correlation between parents and progeny for clupeoid fish. Therefore, many Japanese scientists thought that the impact of fishing had no effect on fluctuations in stock size and that the great changes in the Hokkaido spring herring stock were brought about by natural causes.

Iizuka (1966) sampled larvae in two spawning seasons in his ecological study of the early life of a local herring stock whose spawning grounds were in Akkeshi Bay on the Pacific coast of Hokkaido. Examination of length frequencies of the samples collected showed that the herring that had hatched and grown to larvae were of a single group only, although spawning took place several times from March to June (Fig. 7). The samples were estimated to be from a group that spawned probably

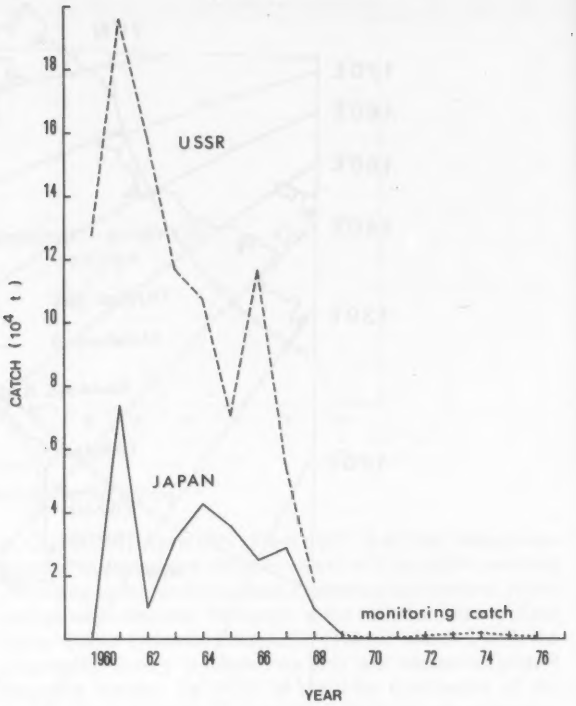

FIG. 6. Annual catch of Korfo–Karaginsk herring by USSR and Japanese fisheries.

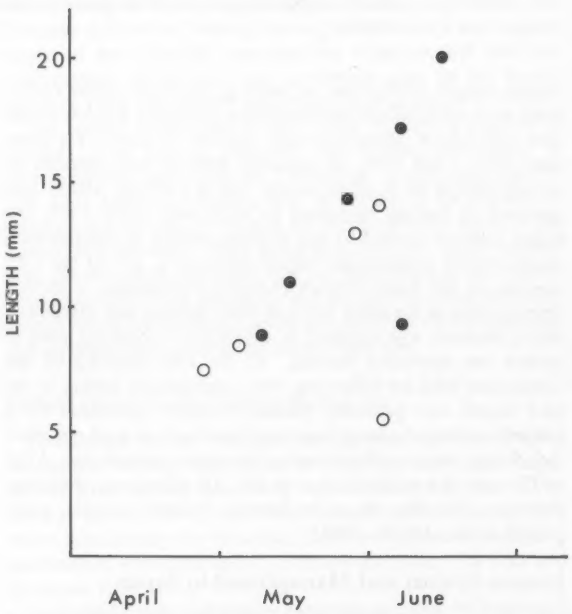

FIG. 7. Modes of length frequency of herring larvae sampled in Akkeshi Bay in 1958 (●) and 1959 (○). (From Iizuka 1966)

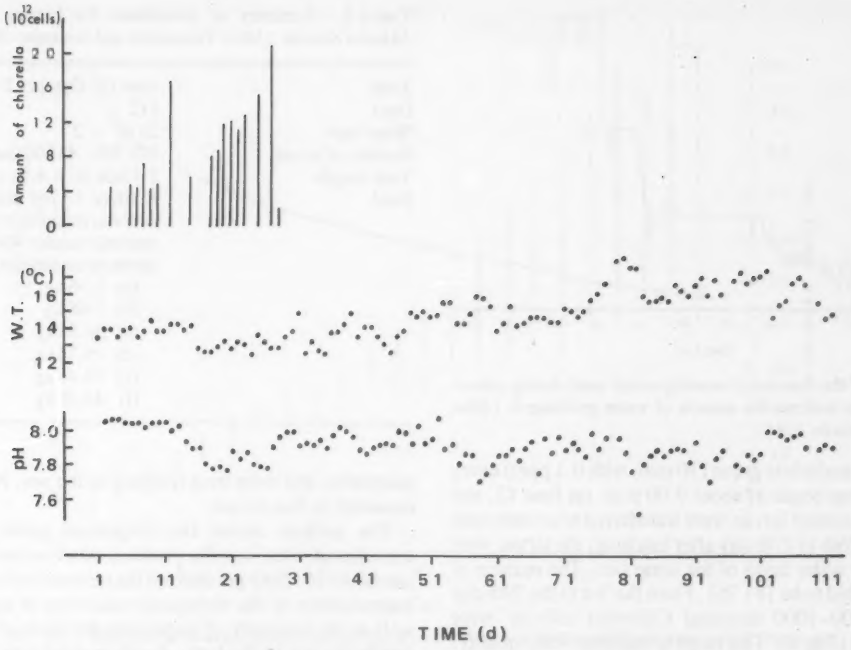

FIG. 8. Changes in the amount of *Chlorella* added to the culture water, with record of temperature and pH. (After Yamamoto and Iwamoto 1983)

between the end of March and the beginning of April in both 1958 and 1959. It was notable that the groups that spawned at other periods of time scarcely survived. By examining the mouth size and stomach contents of the larvae, Iizuka concluded that the survival condition for the larvae was that the start of feeding must correspond with the blooming of copepod food organisms, particularly *Acartia* in Akkeshi Bay. In both years when the surveys were conducted, the larvae from spawning in periods other than the end of March to the beginning of April could not survive because of lack of good feeding conditions after hatching. Conversely, a year-class that was favoured with excellent feeding conditions could turn into a dominant year-class. But, Iizuka argued, because the mortality of larvae is exceptionally high during the period when the larvae are growing to 18 mm in size, and considering the size preference for food organisms, the actual chances of larvae feeding in the natural environment would be very small.

Iizuka's argument explaining the direct relationship between cause and effect concerning fluctuations in stock size is very convincing; however, it is not sufficient to effectively explain the declining trend that has occurred in herring stocks in various parts of Asia. Further examination and discussions will be necessary concerning this problem from a global point of view.

Experimental Trials on Propagation of Herring

Background

In 1982, experiments were successfully carried out at two stations, Akkeshi and Miyako, which belong to JASFA (Japan Sea Farming Association), in which herring juveniles were raised to a size large enough to be released with a surprisingly high survival rate of 46%. Prior to this, artificial hatching has been attempted in Japan to determine the best conditions for hatching (Kuwatani et al. 1978). This was the first trial in which artificially hatched larvae were cultured for the purpose of release and had grown to the juvenile stage with a high survival rate.

This success reflects the remarkable development of artificial seed production technologies in Japan for a variety of marine biomass. These technololgies are characterized by the fact that they have been developed in association with the technical development of marine culture. Such technologies have already been put to practical use in Japan for various species of shellfish and crustacea and also such fish as the red sea bream or Madai (*Pagrosomus unicolor*), the black porgy or Kurodai (*Sparus lingispinis*), the turbot or Hirame (*Paralichthys olivaceus*), and so on. For Madai, in particular, about 2.5 million juveniles are released annually into the sea in coastal areas extending from the central part to the southwestern region of Japan. In some areas, this is correlated with an increase in the catch.

Experiments at Akkeshi Station

The following describes experiments performed at Akkeshi Station (Yamamoto and Iwamoto 1983). The parent fish used for artificial spawning were caught by small trap nets on May 29 in Notoro Lake, a brackish lake situated in the northeastern part of Hokkaido, the spawning ground of a small-scale local herring stock (Fig. 2). Sixty mature female fish and 20 male fish were selected, and artificial fertilization was conducted by the dry method. Approximately 600 000 eggs were used. Fertilized eggs were placed on frames to which palm tree bark was attached. They were covered with cloth soaked in seawater and brought to the station. Transport took about 4 h. The frames were placed in a water tank with a 100-L capacity and running water. The water temperature up to the time of hatching ranged from 5.8 to 9.8°C. During this period, eggs were soaked in

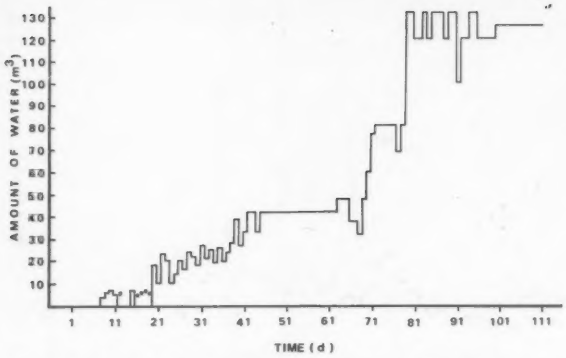

FIG. 9. Record of the amount of running water used during culture period. Solid circles indicate the amount of water exchanged. (After Yamamoto and Iwamoto 1983)

water mixed with malachite green (30 min, with 0.1 ppm) every other day. Hatching began at about 9.00 p.m. on June 12, and immediately the hatched larvae were transferred to a water tank of 20 m^3. On the 26th to 27th day after hatching, the larvae were divided into other water tanks of the same size. The number of larvae was estimated to be 181 761. From the 3rd to the 29th day after hatching, 500–1000 thousand *Chlorella* cells/m^3 were added to the water (Fig. 8). This helps to stabilize water quality. From the 8th day after hatching the water was changed to running water (Fig. 9). The water flow was increased in correspondence with the rise in water temperature as well as the growth of larvae. The variations in water temperature and pH are shown in Fig. 8. Rotifers (*Brachionus plictilis*), *Artemia* (nauplius and adults), and artificial combinations were used for feeding. The size of pellets of artificial bait was increased in parallel with the growth of the larvae. From the 73rd day after hatching, only artificially combined bait was used (Fig. 10). The survival rate and the change in total length during the experiment are shown in Fig. 11. The growth was almost linear and is expressed as $L = 0.6t + 4.364$ ($r = 0.991$) where L = total length (millimetres) and t = number of days from hatch. The formation of scales began at the tail when the total length reached about 28 mm and ended when the length reached 40 mm (except for the dorsal region). The survival rate generally shows a gradually declining curve. There was no critical period in which sharp changes occurred. On the 112th day, the majority of the juveniles were transferred to a net pen in seawater for

TABLE 1. Summary of procedures for herring larval culture at Akkeshi Station. (After Yamamoto and Iwamoto 1983).

Term	June 13–October 2
Days	112
Water tank	20 m^3 × 2
Number of larvae	181 700 – 83 600 (survival rate 46.0%)
Total length	7.4 mm (6.4–8.0) – 66.3 mm
Food	Rotifers: 13 780 million
	Artemia (nauplius): 666 million
	Artemia (adult): 484 million
	Artificial combined bait
	(a) 2.56 kg
	(b) 5.68 kg
	(c) 38.84 kg
	(d) 19.72 kg
	(e) 72.45 kg
	(f) 44.08 kg

adaptation and were then released in the sea. No mortality was recorded in this period.

The authors raised two important points regarding the experiment. One was the problem of a low rate of fertilization (about 30%). They pointed out the necessity of making adequate examinations of the biological conditions of the parent fish, as well as the necessity of improving the method of attaching the fertilized eggs to the bark. Another point was that it would be necessary to use rotifers as food at an early stage, as for other fish species. They pointed out the necessity of developing a standard technique of breeding and raising rotifers of appropriate sizes. The culture process is summarized in Table 1.

Some Considerations

As suggested by Iizuka (1966), whether herring can pass through the critical period in the process of hatching to recruitment probably depends largely on the availability of a suitable food supply during the period following yolk absorption. It is considered that one of the largest determining factors of year-class strength is whether the time of blooming of plankton that can be used as food in the natural environment corresponds with the period following yolk absorption. This suggests the possibility of greater recruitment if the time of hatching of herring could be artificially managed.

In this experiment, parent fish were taken from the population in Notoro Lake, and juveniles were released in Furen Lake

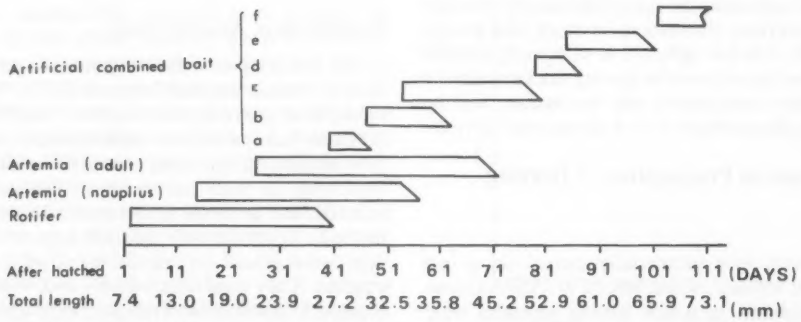

FIG. 10. Sequence in the kinds of food used for larval and juvenile culture. Artificial combined bait (food pellets) was used in the form of larger crumbles for juveniles growth (see Table 1 for reference to lettering). (After Yamamoto and Iwamoto 1983)

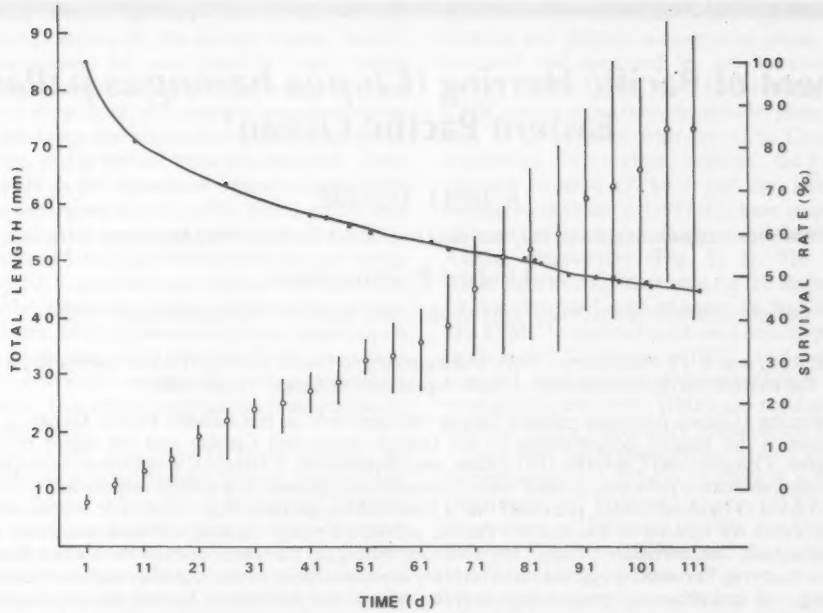

FIG. 11. Percent survival of cultured larval and juvenile stages of herring and their total length (mean ± range). (After Yamamoto and Iwamoto 1983)

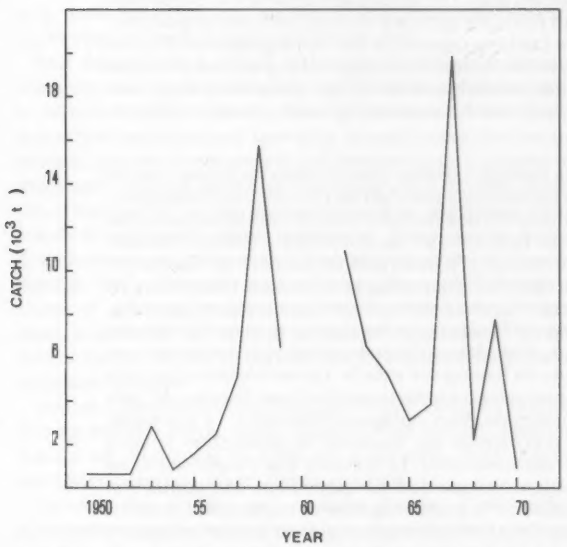

FIG. 12. Annual catch of Akkeshi herring. Data for 1959 and 1960 not available.

(brackish water) facing Nemuro Strait (Fig. 1). However, considering the historical process of the formation of the population, it is considered more desirable that the collection of parent fish and the release of juveniles be done in the same water. A local population of herring is distributed in Akkeshi Bay, where the JASFA station is located. The catches in the area from 1950 to 1969 are shown in Fig. 12 and there has been no commercial fishery in recent years because the population was extremely small. However, considering the fact that there is still a spawning environment that once produced a catch of 20 000 t, it does not seem impossible to attempt to reestablish a larger population of herring through artificial egg production and releases. Workers at the experimental station are currently exerting efforts to collect parent fish in Akkeshi Bay.

Achnowledgments

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Management of Pacific Herring (*Clupea harengus pallasi*) in the Eastern Pacific Ocean[1]

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Pacific herring (*Clupea harengus pallasi*) fishery management in the eastern Pacific Ocean is under jurisdiction of the federal governments of the United States and Canada and the states of Alaska, Washington, Oregon, and California. In Canada, the Department of Fisheries and Oceans is responsible for all Canadian marine fisheries. United States fisheries management is a federal responsibility in waters beyond 5.6 km (3 nautical miles), provided that a Fishery Management Plan is in effect. As no such plan currently exists for herring in the eastern Pacific, individual states manage offshore waters as well as territorial waters. The dominant product from herring fishing on the west coasts of the United States and Canada is "sac-roe," or mature egg skeins, which are used as a caviar product. Other uses include human food, king crab and other commercial bait, bait for recreational fishermen, herring spawn-on-kelp, and animal food. In-season and post-season standing stock estimates are based on direct observation or measurement. Quotas are based directly on standing stock estimates, using one of two philosophies. The first, used mainly in Canada, sets a spawning escapement goal designed to maximize average larval production, and allows harvest of all herring in excess of this goal. The second sets a harvest in proportion to the standing stock, to allow spawning escapement to fluctuate cyclically as in an unfished population. Serious management problems are caused by the large catching capacity of the herring fleets and by the short time period during which satisfactory roe maturity occurs before spawning. Fishing is often limited to several hours or several days, primarily to maintain catches within quota limits, and secondarily to prevent overloading processing facilities. An equitable allocation of the harvest among various users is difficult, compounding management problems.

La gestion de la pêche du hareng du Pacifique (*Clupea harengus pallasi*) dans l'océan Pacifique oriental relève des gouvernements fédéraux canadien et américain ainsi que des États de l'Alaska, de Washington, de l'Orégon et de la Californie. Tandis qu'au Canada le ministère des Pêches et des Océans est responsable de toutes les pêches maritimes, la gestion halieutique aux États-Unis est de compétence fédérale dans les eaux situées au delà de 5,6 km (3 milles nautiques) et pourvues d'un plan de gestion des pêches. Comme un tel plan visant le hareng n'existe pas pour le Pacifique occidental, chaque État gère les eaux hauturières en plus des eaux territoriales. La rogue vésiculée (sacs d'œufs matures), utilisée comme succédané de caviar, représente le principal produit tiré de la pêche du hareng sur la côte ouest des États-Unis et du Canada. De plus, elle sert d'aliment pour les humains et les animaux, d'appât pour le crabe royal ou d'autres espèces commerciales, d'appât pour la pêche sportive et d'œufs de hareng sur varech. Les estimations du stock actuel, pendant et après la saison, sont basées sur des observations ou des quantifications directes. À l'aide de ces estimations, on établit des contingents en fonction de deux optiques différentes. La première, appliqué principalement au Canada, vise un niveau d'échappée qui maximise la production larvaire moyenne et permet l'exploitation de tous les harengs surnuméraires. La seconde fixe l'exploitation en proportion du stock actuel afin de permettre la fluctuation cyclique de l'échappée dans une population non exploitée. De graves problèmes gestionnels découlent de la grande capacité de capture des flottilles de pêche du hareng et de la courte période pendant laquelle la condition de la rogue est satisfaisante avant la fraie. On limite souvent la pêche à quelques heures ou à quelques jours, principalement afin de maintenir les prises en deçà des limites du contingent et d'empêcher la surcharge des usines de traitement. La difficulté que représente une répartition équitable de la prise parmi les divers usagers vient ajouter aux problèmes gestionnels.

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Pacific herring (*Clupea harengus pallasi*) have a long history of exploitation in the eastern Pacific Ocean. Herring and herring roe were taken by many Indian groups along the coast for centuries. Herring rakes and dip nets were used in deep water, with traps and mazes along the shoreline. Tribes used eggs and whole herring, fresh and dried, for food and trading, and as bait for birds and other fish. Since the arrival of settlers in the nineteenth century, commercial herring fishing has undergone several cycles. Dried, salted, and smoked products, reduction to oil and meal, and bait for commercial and recreational fishing have been dominant uses during past periods. Since 1973, most herring landings have been used for sac-roe (sexually mature egg skeins), a caviar-like product important in the Orient. Herring roe-on-kelp (eggs deposited on marine vegetation) is also harvested along the Pacific coast. Bait uses continue on a small scale, and minor quantities are used for human consumption. This review emphasizes management of roe fisheries through 1982.

Herring fisheries on the west coast of North America are currently or potentially managed under several jurisdictions. Within the United States, the states of California, Oregon, Washington, and Alaska each have responsibility within state waters (0–5.6 km (0–3 nautical miles)). The U.S. Department of Commerce (USDC) has federal management authority in the Fishery Conservation Zone (FCZ) from 5.6 to 370.6 km (3–200 nautical miles). Within British Columbia, the Department of Fisheries and Oceans (DFO) has management authority for all herring fisheries. Each jurisdiction faces various biological (e.g. stock assessment) and socioeconomic problems of allocating herring between competing harvest users.

One distinguishing feature of eastern Pacific coast herring management is a reliance on direct observation or measurement to estimate herring biomass. Two of the most common direct assessment techniques are spawning ground surveys to directly estimate spawning escapement and hydroacoustic estimates of abundance. Indirect techniques involving catch per unit effort, cohort analysis, or surplus production models, when used, serve mainly to supplement direct assessment. Catch quotas are set from assessments using one of two philosophies. In Canada through 1982, allowable harvest for an area was all herring in excess of spawning escapement judged to produce the maximum amount of larvae (i.e. optimum escapement). In the United States, allowable harvest was a proportion of the total estimated biomass.

British Columbia has produced the largest catches since roe herring fisheries began, with Alaska a close second, although Alaska led production in 1980–82. California, Washington, and Oregon produce lower quantities (Table 1).

Articles that review and evaluate Pacific coast herring management practices occur mainly as unpublished documents or publications with limited distribution; few can be found in the primary literature. The following sources provide detailed management overviews: Melteff and Wespestad (1980), NPFMC (1983), PFMC (1982), Spratt (1981), Hourston (1980a, 1980b), Walters et al. (1982), and Buchanan (1983).

Management Infrastructure

Along the west coast of the United States, marine fisheries have traditionally been managed by the individual states. In 1976, the U.S. Congress passed the Magnuson Fishery Conservation Management Act (MFCMA), which extended United States jurisdiction to a FCZ of 5.6–370.6 km (3–200 nautical miles). The MFCMA established regional councils to monitor fisheries and prepare management plans. All plans must be reviewed and approved by the National Marine Fisheries Service (NMFS) and USDC before being enacted by USDC. USDC passes regulations required by plans; NMFS administers and, in cooperation with the U.S. Coast Guard, enforces regulations. Two regional councils, the Pacific Fishery Management Council (PFMC) and the North Pacific Fishery Management Council (NPFMC), have responsibility for waters adjacent to Washington, Oregon, and California and adjacent to Alaska, respectively (Fig. 1, 2). The NPFMC has been preparing a management plan for the Bering–Chukchi Sea but has not scheduled work on a plan for the Gulf of Alaska region. The PFMC terminated work on a herring plan for Washington, Oregon, and California in 1982. Until management plans are accepted, management of domestic fisheries in offshore waters remains with the states; NMFS can regulate foreign fisheries in the FCZ with a Preliminary Management Plan.

Each state has a management agency with responsibility for herring within the 5.6-km (3 nautical mile) limit: the Alaska Department of Fish and Game (ADFG), the Washington Department of Fisheries (WDF), the Oregon Department of Fish and Wildlife (ODFW), and the California Department of Fish and Game (CDFG) (Fig. 1, 2). Each state except Washington has a citizen board or commission that makes decisions on policy matters such as allocation or utilization. In Washington, policy is made by WDF within constraints set by the legislature. Management practices by respective state agencies follow established policies.

In Canada, policy and strategic planning for the British Columbia herring fishery is the responsibility of the federal DFO and is carried out in consultation with various user groups through a recently formed Minister's Advisory Council and through the Herring Industry Advisory Board. Management responsibility of DFO includes both territorial waters and the extended jurisdiction of Fishing Zones of Canada to 370.6 km (200 nautical miles) (Fig. 3).

The multitude of agencies, boards, or councils involved in management or policy decisions for herring fishing in the eastern Pacific is a potentially severe jurisdictional problem. However, all fishing at the present time occurs in inshore waters, leaving actual management to state agencies or DFO. Transboundary migration, and possible fishery interception, occurs along the Alaska–Canada boundary and along the Canada–Washington boundary. No jurisdictional disputes have occurred, but may develop if interest in offshore herring fishing increases.

Description of the Fisheries

Herring is predominantly a commercial species along the Pacific coasts of the United States and Canada. The amount taken by recreational fishermen for personal use, though not quantified, is so small that management of this harvest is a minor consideration.

Historically, most herring landed in the Northeast Pacific were utilized for reduction to oil and meal in domestic plants; large amounts have also been caught by foreign fleets. In the Gulf of Alaska, reduction fishing peaked in 1937, and declined until the last reduction plant closed in 1966 (Reid 1971). Reduction fishing in British Columbia reached a peak during the early 1960s, but plummeted when stocks crashed in the late 1960s (Hourston 1980a) (Table 1). Foreign fishing in the Bering

TABLE 1. Catch (metric tons) of Pacific herring in the eastern Pacific Ocean, 1960–82.[a]

	California			Oregon			Washington			British Columbia			Gulf of Alaska			Bering Sea		
Year	Roe	Other	Total	Roe	Other	Total	Roe	Other	Total	Roe	Other	Total	Roe	Other	Total	Roe	Other	Total[b]
1960	—	817	817	—	4	4	—	1862	1862	—	181 621	181 621	—	35 341	35 341	—	10 403	10 403
1961	—	636	636	—	8	8	—	1634	1634	—	183 661	183 661	—	22 437	22 437	—	10 572	10 572
1962	—	592	592	—	7	7	—	2888	2888	—	219 203	219 203	—	15 367	15 367	—	24 763	24 763
1963	—	286	286	—	7	7	—	3162	3162	—	264 007	264 007	—	14 159	14 159	—	47 060	47 060
1964	—	158	158	—	15	15	—	1796	1796	—	261 737	261 737	514	21 215	21 729	18	39 812	39 830
1965	—	234	234	—	23	23	—	3786	3786	—	238 297	238 297	596	11 033	11 629	—	10 896	10 896
1966	—	110	110	—	42	42	—	2048	2048	—	180 340	180 340	2 518	6 205	8 723	11	8 385	8 396
1967	—	123	123	—	38	38	—	2925	2925	—	129 928	129 928	1 508	3 584	5 092	122	7 714	7 836
1968	—	162	162	—	17	17	—	2925	2925	—	14 207	14 207	1 832	1 774	3 606	82	60 622	60 704
1969	—	77	77	—	35	35	—	3763	3763	—	1 813	1 813	2 569	3 344	5 913	45	129 437	129 482
1970	—	143	143	—	20	20	—	2004	2004	—	2 922	2 922	4 673	3 336	8 009	32	145 547	145 579
1971	—	109	109	—	12	12	—	1717	1717	—	10 742	10 742	1 857	2 722	4 579	18	46 130	46 148
1972	—	52	52	—	12	12	150	1457	1607	34 596	9 303	43 899	3 792	1 855	5 647	89	60 458	60 547
1973	949	310	1 259	—	19	19	1900	1230	3130	50 960	10 379	61 339	10 298	3 600	13 898	78	36 274	36 352
1974	2 285	94	2 379	—	26	26	3953	1554	5507	43 505	5 283	48 788	10 801	3 894	14 695	114	25 435	25 549
1975	948	150	1 098	—	32	32	3595	2365	5960	53 293	5 623	58 916	10 914	5 610	16 524	51	16 015	16 066
1976	2 135	51	2 186	—	35	35	1989	1601	3590	78 832	14 394	93 226	8 995	5 165	14 160	8	30 627	30 635
1977	4 444	67	4 511	—	25	25	2088	936	3024	73 485	15 376	88 861	7 692	5 848	13 540	2 545	18 737	21 282
1978	5 215	33	5 248	—	63	63	1921	1012	2933	63 408	27 984	91 392	4 938	5 006	9 944	7 303	8 983	16 286
1979	4 218	56	4 274	45	34	79	1741	1782	3523	37 480	21 224	58 704	8 611	4 009	12 620	11 745	6 796	18 541
1980	6 449	55	6 504	48	16	64	1434	1739	3173	16 414	3 197	19 611	13 837	3 934	17 771	26 800	410	27 210
1981	5 842	105	5 947	41	26	67	—	1163	1163	29 486	7 961	37 447	20 928	2 403	23 331	17 652	639	18 291
1982	10 270	272	10 542	5	52	57	397	700	1097	34 000	6 244	40 244	14 894	2 182	17 076	25 355	3 234	28 589

[a]Data from management agencies.
[b]Through 1979, most "other" catches are from Soviet and Japanese fleets.

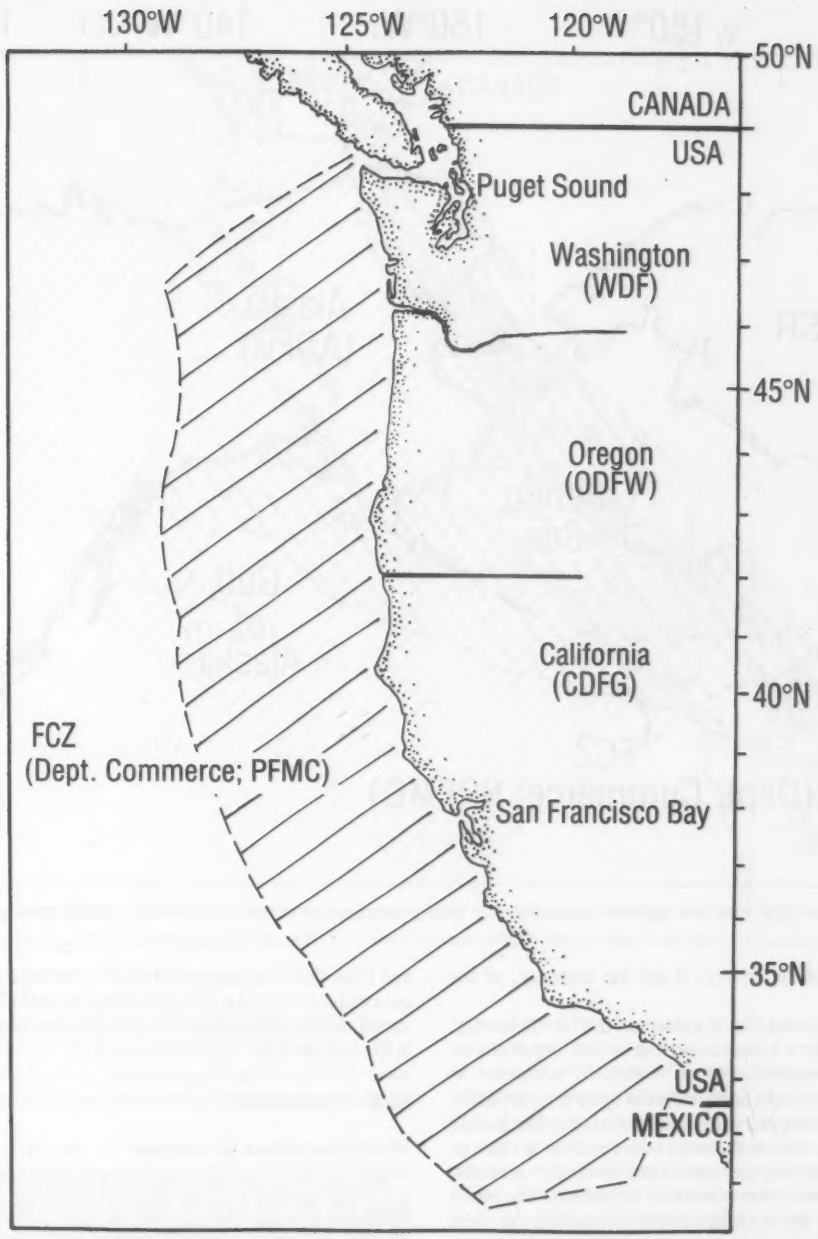

FIG. 1. Fishery conservation zone and agencies responsible for fishery management in waters adjacent to Washington, Oregon, and California (management agencies in parentheses).

Sea expanded rapidly through the 1960s, and then generally declined (Table 1) until directed foreign harvest was prohibited in 1980 (NPFMC 1983).

Fisheries for sac-roe produce the largest commercial herring harvest in the eastern Pacific (Table 1). Purse seines and gill nets are the main fishing gear coastwide, although lampara nets are important in California. These fisheries target on sexually mature, prespawning herring; the sac-roe, or egg skein, is removed and processed into Kazunoko, a caviar product important in Japan. Eastern Pacific sac-roe fisheries developed in the early 1970s when traditional supplies of herring to Japan dwindled. Canadian herring supplied most of the market in the early years, but Alaska and California have increased their market shares in recent years. Interest in the sac-roe fishery grew rapidly as high demand increased ex-vessel prices. In 1979, prices peaked 10–20 times higher than values at the beginning of the fishery in 1972–73, and a "gold rush" atmosphere developed. In 1980, however, the Japanese roe market nearly collapsed as consumers boycotted the product because of artificially high prices. The resulting price drop of

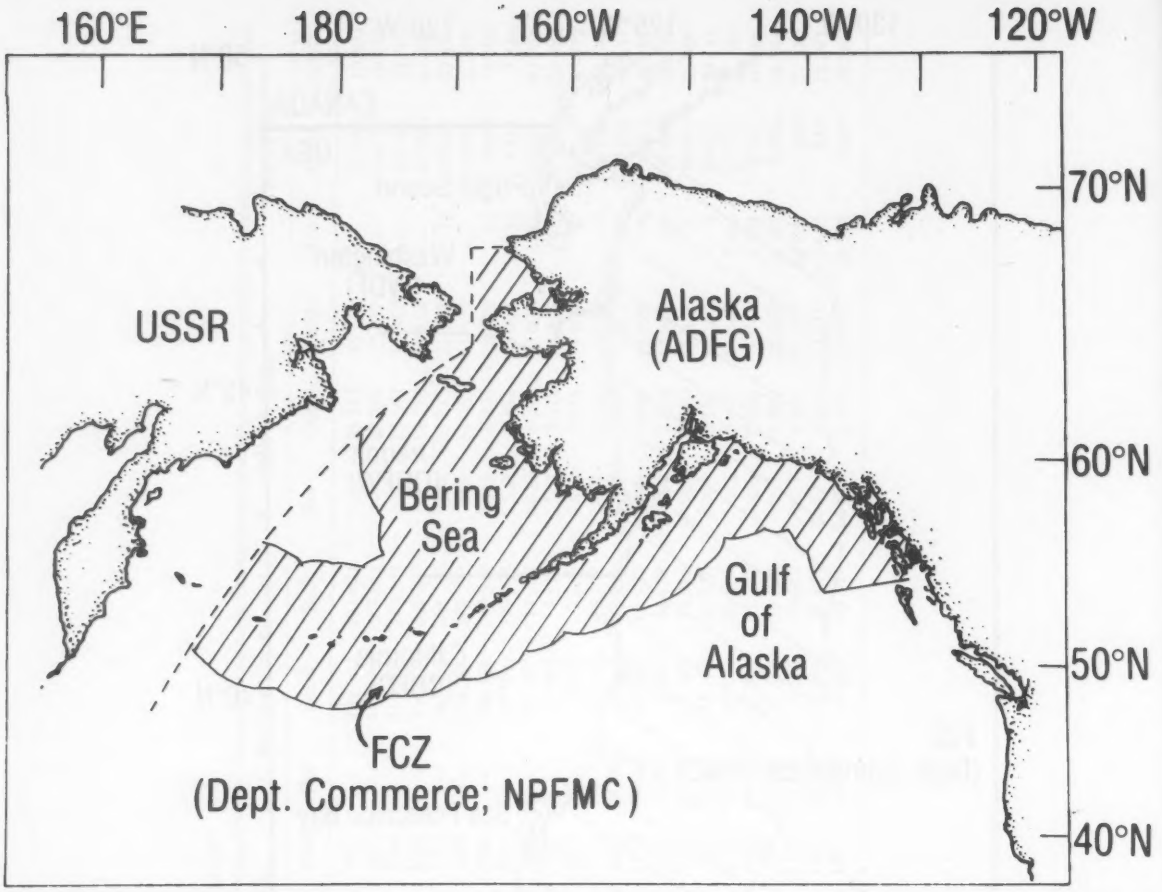

FIG. 2. Fishery conservation zone and agencies responsible for fishery management in waters adjacent to Alaska (management agencies in parentheses).

75% or more reduced the frenzy, if not the intensity, of the fisheries.

Roe-on-kelp is harvested in California, British Columbia, and Alaska. This fishery harvests herring spawn deposited on naturally occurring vegetation or on vegetation suspended in impoundments or from rafts installed near spawning grounds. The remainder of herring harvests are used mainly for human consumption and bait. These fisheries occur mainly in fall and early winter as herring migrate toward the spawning grounds, before fat reserves have been converted to gonads. The small size of Pacific herring and the high cost of transporting the more suitable Bering Sea herring limit the demand for these fish on the European market. Canada made a serious effort to penetrate the food herring market, but without success. Herring make desirable bait for commercial pot and long line fishing; the king crab fishery has used most of the commercial grade bait. Value of food herring and bait herring remains well below prices of roe herring.

A unique small fishery supplies "sport bait" to recreational fishermen. Herring are transported live from the fishing ground in vessels with tanks, and held live in pens until sale or processing. A wide variety of gear, including purse seine, lampara, dip net, and beach seine, is used in this fishery, which targets on small (120–150 mm SL) immature herring. Live bait and fresh dead bait are preferred by recreational fishermen, but are available only at a limited number of outlets. Price per pound varies considerably, depending on fish size and whether the bait is fresh or frozen.

Stock Assessment

Direct Assessment Techniques

The characteristic movement of Pacific herring into nearshore areas for several days to several weeks before spawning on marine vegetation facilitates direct measurement of biomass. Overflights and hydroacoustic surveys are used to estimate prespawning biomass; egg deposition densities can be converted to estimates of spawning escapement; tagging and recovery studies on the spawning grounds provide information on stock identity and movement patterns; biological samples and catch records for stock assessment and population dynamics match easily to specific stocks and areas.

Spawning ground surveys

Pacific herring deposit their eggs on vegetation found in intertidal and shallow subtidal areas of bays, inlets, and estuaries. Investigators from California to Alaska have developed techniques to measure the abundance of spawn as a direct

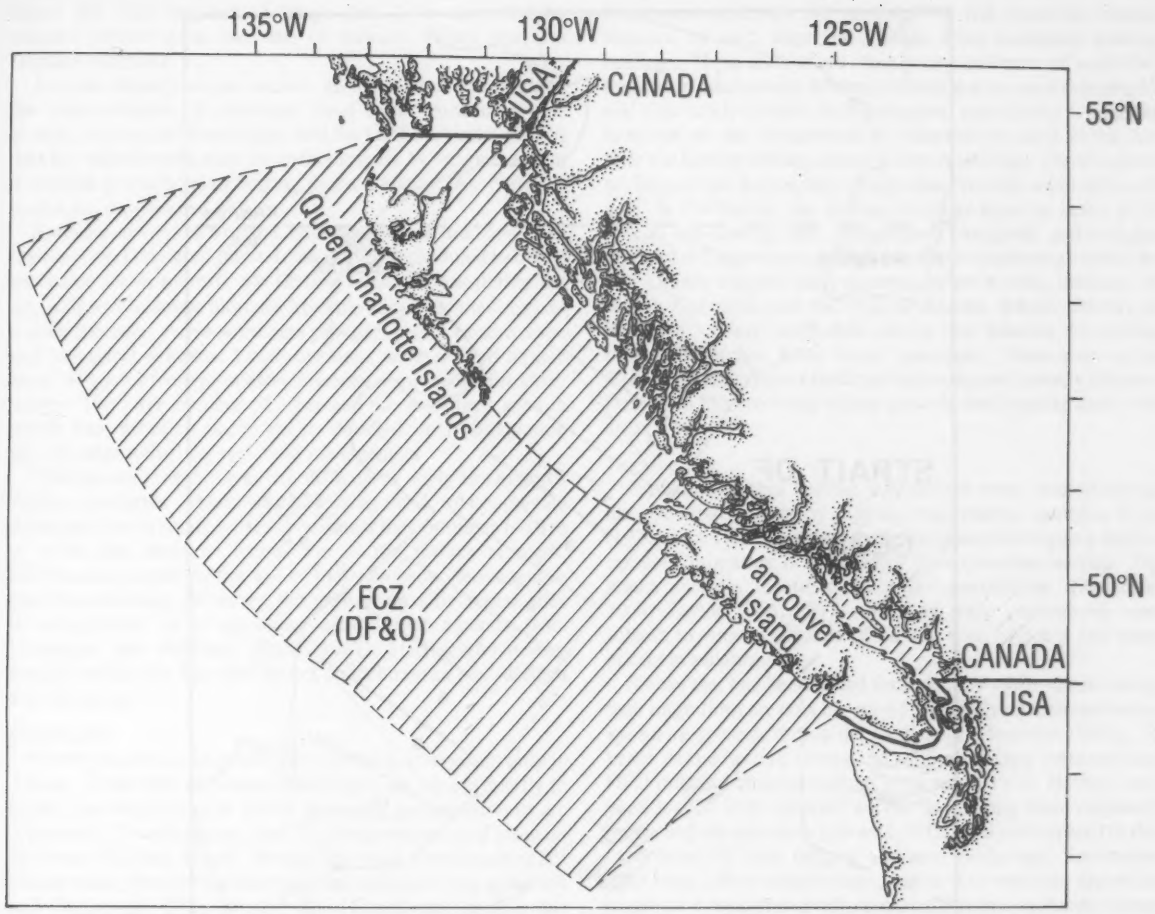

FIG. 3. Fishery conservation zone and agency responsible for fishery management in waters adjacent to western Canada (management agency in parentheses).

estimate of spawning escapement (Trumble et al. 1977; Humphreys and Hourston 1978; Blankenbeckler 1980; Spratt 1981). Unless otherwise indicated, "spawning escapement" will mean biomass of spawning herring estimated directly from spawning ground surveys.

Initially, lineal extent of intertidal spawning along the shoreline was recorded at low tide by walking the beach or from a small boat close to shore. Information on intensity and width of submerged spawning may be obtained by pulling a grappling device known as a "spawn rake" through the vegetation beds on which herring may spawn. These data were plotted on marine charts, lineal distance measured, and results used as an index of relative spawning escapement. Information on mean fecundity, vegetation density, and mean spawning width, and spawn intensity (egg density on vegetation) allowed conversion of lineal distance to absolute biomass (Hourston et al. 1972).

Improvements to spawning escapement estimation involve estimating total number of eggs and converting total eggs to fish biomass with area-specific fecundity. In California, grappling is used to estimate surface area of spawning and to obtain samples of vegetation for calculation of eggs per unit weight of vegetation; these results are converted to total eggs, and total eggs to spawning biomass (Spratt 1981). For spawnings that occur on nonvegetated areas, eggs are removed from quadrat subsamples of the normally rocky bottom. In British Columbia, vegetation maps prepared using diver transects and aerial photography and density of eggs estimated by diver surveys or by spawn rake are combined with area-specific fecundity to estimate total spawning escapement (Humphreys and Hourston 1978). A diver transect method is also used in many areas of the Gulf of Alaska (Blankenbeckler 1980). Spawning ground surveys have not been used for stock assessment in the Bering–Chukchi Sea because of the remote location and large area in which herring spawn (Barton and Wespestad 1980). However, ADFG is currently exploring application of this technique to specific areas (S. Fried, ADFG, Anchorage, AK, pers. comm.).

Hydroacoustics

Quantitative hydroacoustic surveys for Pacific herring stock assessment began during 1969 in southeast Alaska (Blankenbeckler 1980) and 1971 in Washington (Lemberg 1978) and became an integral part of stock assessment for herring management in the mid-1970s. Principles and techniques of

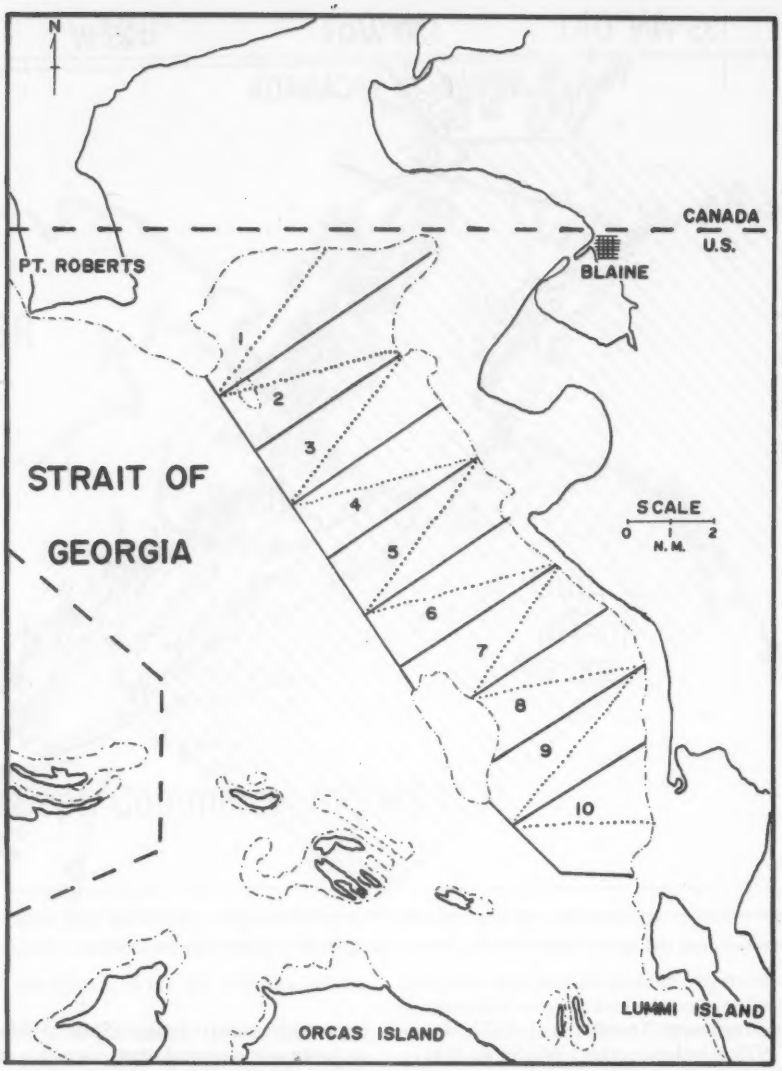

FIG. 4. Strait of Georgia standard acoustic trackline pattern (---). Solid lines and 10-fathom contour (---) define survey subareas (from Lemberg 1978). N.M. = nautical miles.

echo integration used to quantify herring biomass are given by Thorne (1977a, 1977b). Biologists in Washington and the Gulf of Alaska rely more on hydroacoustics than biologists in other regions.

In Washington, for example, herring fished for roe in the Strait of Georgia immigrate into a holding area, reach an abundance peak, move inshore to spawn, and then disperse. Hydroacoustic surveys conducted since 1976 during April and May bracket this herring spawning migration (Lemberg 1978). Surveys conducted between Point Roberts and Lummi Island follow a standard trackline with 10 transects, each approximately 8 km in length (Fig. 4). Surveys are usually conducted twice each week during the peak of migration, and less frequently during early and late stages of the run.

During the day, prespawning herring normally aggregate in dense schools but disperse at night to form widespread lower density layers. Surveys are conducted at night because herring are more uniformly distributed and farther off bottom.

In the Gulf of Alaska, acoustic transects also cover herring concentration areas, but often herring must first be located by searching (Blankenbeckler 1980). Gulf of Alaska herring tend to disperse into near-surface or nearshore areas at night, so cannot regularly be surveyed at night. Daytime surveys are confounded by high density of herring schools. Surveys are usually conducted at dawn and dusk, between high density schooling and dispersion (Thorne et al. 1982).

Acoustic data from Washington and the Gulf of Alaska are integrated by computer processing for density (kilograms per cubic metre) at preselected depth intervals for each transect. Integration values are scaled to biomass using a mean target strength of -33 dB/kg. Depth interval densities are accumulated to calculate an average density (kilograms per square

metre) for each transect. Average density is expanded by transect surface area; the sum of transect values provides biomass estimates.

Acoustic density values include all fish detected throughout the water column. A midwater trawl series conducted with acoustic surveys in Washington and the Gulf of Alaska obtains data for apportioning total acoustic biomass by species, and to determine proportions of herring that are mature (roe herring), immature, or spawned out.

Acoustic surveys in British Columbia are used in a semiquantitative way. Chartered purse-seine vessels, scheduled to fish in particular areas, traverse the herring holding areas during the day; skippers estimate biomass from the density of markings on a chart recorder. Purse-seine sets provide species confirmation and biological samples. Local openings were set and adjustments of quotas from preseason forecasts were made from these results. The large number of areas and the short time span in which roe fisheries occur make detailed echo integration surveys impractical for real-time management.

Hydroacoustic techniques are difficult to apply in Oregon's shallow estuaries. Prespawning herring tend to congregate during the day in small dense schools near the bottom in 7–10 m of water and move to within 5 m of the surface at night. California is exploring the use of hydroacoustic assessment in San Francisco Bay. However, the application of hydroacoustics is complicated by a spawning season that extends from November into February (Spratt 1981). Herring move very quickly within the Bay and do not concentrate in well-defined holding areas.

Overflights

Overflights are used extensively for stock assessment only in Alaska. In the Gulf of Alaska, overflights are used primarily to locate spawning areas in which spawning ground surveys are conducted. Overflights are used for direct estimates of biomass in Prince William Sound. Bering Sea stock assessment relies almost totally on overflights to estimate herring biomass (Barton and Wespestad 1980; Fried 1983). Overflights became the primary tool because other techniques were judged impractical. Approximately 1000 km of remote shoreline subject to extreme weather conditions make spawning ground surveys difficult. Acoustic surveys could not be used in nearshore areas because of shallow water depths, widespread distribution of herring schools, a long spawning season, and the lack of known holding areas in which stock would congregate.

Bering Sea overflights involve recording the number of fish schools by surface area in selected coastal spawning areas. Counts are adjusted to a standard surface area (50 m^2) and converted to biomass by using a density range (tons per square metre) derived from purse-seine catches within known water depths. Total biomass estimated by overflights is adjusted by results of test fishing to compensate for other fishes (mostly capelin, boreal smelt, and saffron cod), which occur with the herring. Peak daily biomass for the season is used as the best estimate of spawning stock. Daily biomass estimates may be summed if sampling identifies different groups of spawning herring, based on factors such as age composition and sexual maturity indices.

Catch records

Although catch records are insufficient by themselves for in-season stock assessment, they form an integral part of the post-season roe herring assessment and must be obtained quickly in-season to prevent harvests from exceeding quotas. Final catch statistics are provided by fish receiving tickets required by each state and Canada from fishermen making landings. These records are often not completed until well after the season, and several different techniques are used to maintain real-time catch records. In Washington, each dealer is required to telephone the Department of Fisheries by noon of the day after roe herring fishing ceases to report landings. These reports are logged into a computer system that provides rapid access to data. In California, roe herring landings must be made at an official off-loading site, immediately weighed, and weights reported to Department of Fish and Game representatives at the site. Oregon requires daily reporting of roe herring landings. In British Columbia and the Gulf of Alaska, fishery officers or biologists collect catch data during roe fisheries by hailing estimated catches from vessel operators. Processors in the Bering Sea must report landings following each fishery closure. Data from fish receiving tickets provide final landing data in all areas.

Tagging

British Columbia herring populations were studied during the reduction fishery by tagging experiments spanning 31 yr (1936–67). The reduction fishery and associated tagging studies involved migrating herring rather than spawning herring. Tag return analysis identified 13 major populations (Stevenson 1954; Taylor 1964, 1973). Most of these populations were subject to various degrees of mixing with adjacent and more distant populations.

Stocks that had been fished for reduction while mixed during their migrations are now harvested separately on their individual spawning grounds during the roe fishery (Hourston 1980a). To better define herring stocks and estimate fishery interceptions, DFO initiated another tagging program in 1979. Herring have been tagged with external anchor tags along their migratory routes and on spawning grounds. WDF also participated in this experiment by both tagging and recovering tags. Recoveries have been below expectations, but several separate spawning stocks have been tentatively identified that mix on Pacific Ocean feeding grounds and during migration to spawning grounds (Haegele et al. 1983). Transboundary migrations occur between Alaska and British Columbia and between British Columbia and Washington.

Population parameters

Biological samples obtained from commercial catches and research surveys provide basic data for calculating age composition, growth, maturity, and mortality. In general, herring populations at the southern extremes of their range tend to have younger, earlier maturing herring with higher growth rates, while older, later maturing herring with lower growth rates tend to the north (PFMC 1982; NPFMC 1983).

Herring normally recruit to the spawning population, and thus to the roe fishery, at ages 2–6 (PFMC 1982; NPFMC 1983). In San Francisco Bay the spawning biomass consists largely of 2- and 3-yr-old herring, and 2-yr-olds make a strong contribution. Since 1980, 2-yr-old herring have formed a major proportion of the spawning biomass in the Washington roe fishery, although in previous years 2-yr-old herring were rarely present, and most fish were aged 3–6. Most British Columbia and Alaska herring recruit at ages 3–5.

Pacific herring generally grow rapidly through age 3 or 4, and growth tapers off significantly in later years (PFMC 1982; NPFMC 1983). Von Bertalanffy growth parameters indicate that the exact pattern varies along the coast. San Francisco Bay

contains the fastest growing (K = 0.59) yet smallest (L_∞ = 208 mm) of the major stocks. The eastern Bering Sea herring are the slowest growing (K = 0.18–0.35), and largest (L_∞ = 299–314 mm).

Natural mortality rates are difficult to assess because most stocks also experience fishing mortality. Time series are often too short to provide good estimates. Most estimates of instantaneous natural mortality rates (M) fall very consistently in the range 0.4–0.5. Wespestad (1982) estimated average M in the eastern Bering Sea at 0.39 using Alverson and Carney's (1975) method; however, age-specific M values ranged from 0.15 to 0.36 when estimated by subtracting an assumed F from total mortality (Z) calculated from catch data. Natural mortality in the Strait of Georgia, Washington, was estimated at 0.40 by subtracting an estimated average M of 0.22 from a Z estimate of 0.62 using regression techniques (R. J. Trumble, unpubl. data). Other Puget Sound, Washington, stocks, unexploited as adults, have Z estimated at 0.50 (Gonyea and Trumble 1983).

Data Combinations

Biomass estimates

Nearly all biomass estimates result from combinations of several different stock assessment techniques. The most commonly used estimate is the postseason total of spawning escapement (estimated from spawning ground surveys) plus catch. This technique is not used in the Bering Sea or Prince William Sound. California and Oregon use escapement plus catch as the only biomass estimate. Canada considers escapement plus catch as the best estimate, which subsequently forms the basis for stock assessment.

Washington combines hydroacoustic stock assessment with spawning escapement plus catch to calculate a series of point estimates prior to and through the fishing season (Trumble et al. 1982). Acoustic–trawl surveys carried out at regular intervals during the spawning season monitored declines of prespawning herring biomass; the declines correspond to cumulative increases of catch plus spawning escapement. From the time of full entry of adult herring to the fishery, the sum of cumulative catch, cumulative escapement, and acoustic–trawl estimates provided point estimates of total available adult herring. From 1976 to 1980, the in-season point estimates varied less than 15%. However, in 1981 and 1982 the acoustic–trawl estimates greatly exceeded the final escapement plus catch estimates, by more than double in 1982 (Trumble 1982).

Blankenbeckler (1982) summarized spawning escapement plus catch and hydroacoustic biomass estimates from 1978 through 1980 in southeast Alaska. In many cases, spawning escapement plus catch and hydroacoustic biomass estimates were not done for the same area. For areas with both estimates, acoustic values regularly exceeded escapement plus catch. Some differences may have resulted from quantities of nonspawning herring included in acoustic surveys. More recently, distribution of prespawning herring has changed so acoustic surveys cannot completely estimate total biomass, and spawning ground surveys have become the main source of data.

Cohort analysis

Although direct measurements have traditionally provided herring stock assessment estimates for the eastern Pacific, cohort analysis (Pope 1972) has recently been used in efforts to validate direct techniques. Canadian spawning escapement plus catch estimates have been compared with cohort analysis results (Schweigert and Hourston 1980; Hourston and Schweigert 1980; Walters et al. 1982). Catch at age data were obtained from sampling commercial harvests (Hourston and Hamer 1979). Cohort analysis consistently produced abundance estimates higher than those obtained from spawning escapement plus catch, except for statistical areas with low cumulative fishing mortality. The investigators concluded that differences did not invalidate the direct assessment techniques. Also, cohort analysis could only be used for pooled fishing areas because needed data were not available for smaller management units, while the smaller areas could be assessed with direct methods.

Cohort analysis of Bering Sea catch data (Wespestad 1982) also provided estimates of age composition and biomass. Analyses were based on data from the foreign fishery in earlier years, and from the domestic roe herring fishery more recently. Age composition estimated from the cohort analysis agreed favorably with age composition observed in 1979–81 during the roe fishery (Wespestad 1982). Cohort analysis estimated total biomass within the range estimated by overflights, but was less variable than overflight estimates (S. Fried, ADFG, pers. comm.).

Abundance forecasts

A combination of stock assessment and biological data is used in Canada to forecast stock abundance and available roe harvest (Hourston and Schweigert 1981). Expected returns of spawners for each year are calculated from estimates of survivors from the previous year and recruitment of virgin herring. Survivors are calculated by decrementing estimated numbers of spawning fish at age by natural mortality and converting numbers to biomass using mean weight at age. Average recruitment from past years is added to survivors to estimate total run size. Subtracting desired spawning escapement from total run size leaves the predicted quota.

Actual postseason spawning escapement plus catch has compared poorly with preseason predictions. However, improved comparisons occurred when predictions were hindcast for earlier years using refinements in methods and updated biological data (Hourston 1981).

The "Hourston" forecast method is now being supplemented in British Columbia with age-structured and surplus production analyses (Stocker et al. 1983). Age-structured analysis uses the Fournier and Archibald (1982) model and incorporates biological, commercial catch, and spawning escapement data along with stochastic processes. Surplus production analysis assumes that production is the difference between spawning escapement plus catch of a given year and survivors from the previous year. All three methods produce similar long-term abundance trends, but forecasts must still be evaluated (Stocker et al. 1983).

Population trends

The problem of stock identification has not yet been resolved for Pacific herring, but each spawning area that supports a commercial fishery is managed as if it contained a genetically distinct stock.

In California there are about 12 known spawning areas; of these, only 2, Tomales Bay and San Francisco Bay, support major herring populations (Spratt 1981). Both areas support roe herring fisheries managed at a conservation rate of exploitation (less than 20%). The increasing trend (Fig. 5) in population size is attributed to improved spawn survey coverage and methodology, which added subtidal spawning areas and earlier spawnings as they became known (Spratt 1983).

Oregon has little herring spawning habitat and small stocks.

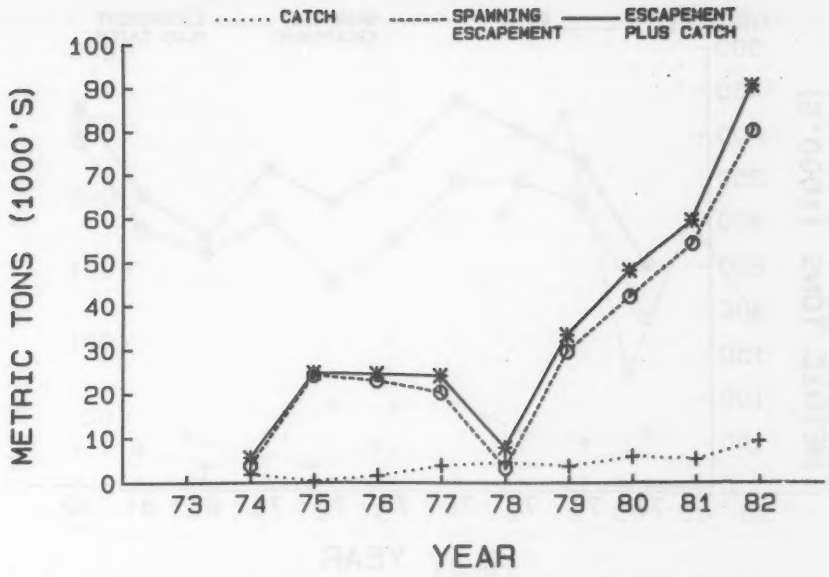

FIG. 5. Stock assessment and population trends for Pacific herring in San Francisco Bay, California.

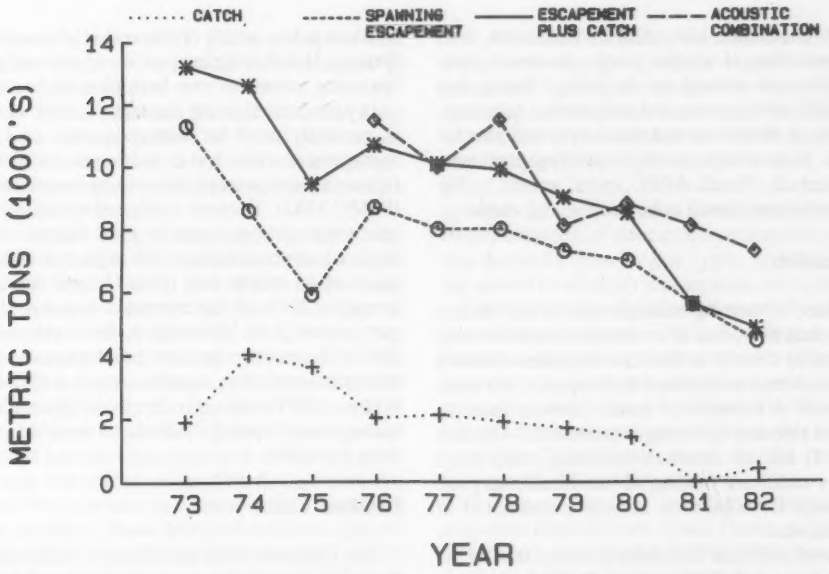

FIG. 6. Stock assessment and population trends for Pacific herring in the Strait of Georgia, Washington.

Harvests for bait and roe are kept small, and although abundance fluctuates, the abundance is apparently stable.

In the northern Puget Sound – Strait of Georgia area of Washington, stocks have been declining in recent years (Fig. 6) and the roe herring fishery has been curtailed (Trumble 1982). The decline has apparently been caused by natural fluctuations, although increased by the effects of fishing: since three strong year classes were recruited at the beginning of the fishery in 1973, only two strong year classes have recruited subsequently (Trumble 1983).

In southern British Columbia, herring stocks in the Strait of Georgia appear to be stable and strong, but on the west coast of Vancouver Island, stock size in 1982 was substantially lower than the 10-yr mean (Stocker et al. 1983). Northern British Columbia herring stocks generally appear to be stable, with 1982 populations as high as the maximum recorded during the previous 10 yr. Overall, British Columbia herring show no long-term trends (Fig. 7).

In the Gulf of Alaska, larger stocks have fluctuated in abundance since the start of the roe fishery, but appear to be in

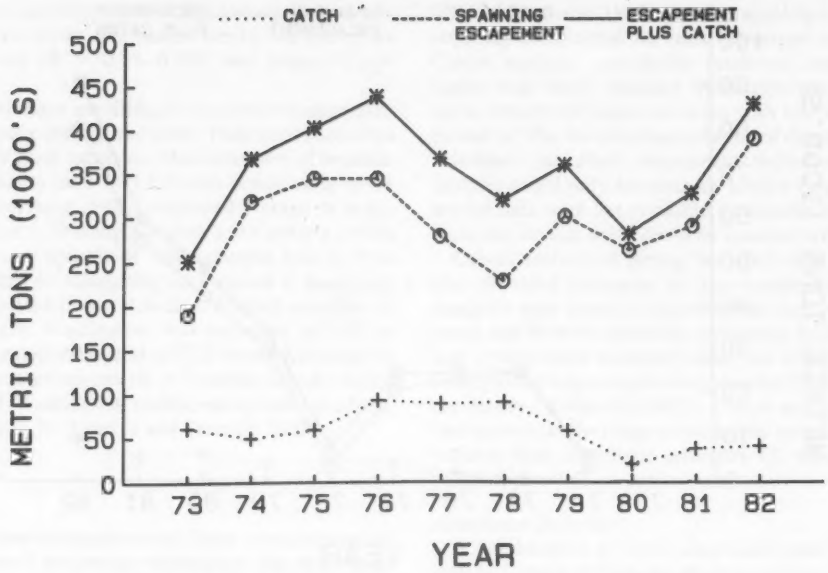

FIG. 7. Stock assessment and population trends for Pacific herring in Canada.

good condition (D. Blankenbeckler, ADFG, Ketchikan, AK, pers. comm.). Populations of smaller stocks, however, have been highly variable, and several are declining. Bering Sea herring have been difficult to assess, and only limited data exist. Extreme fluctuations in abundance estimated by overflights for the Bering Sea (Fig. 8) have been caused by sampling problems, often weather-related (S. Fried, ADFG, pers. comm.). The population is generally considered to be healthy and viable.

Quota Determination

A common feature of herring management in the eastern Pacific is establishment of quotas to set harvest levels. In most cases, quotas are based directly on biomass estimates obtained from previously mentioned assessment techniques. Two basic strategies have been developed to match harvest rates to observed population size and spawning requirements. The first of these (Strategy I) sets an optimum spawning escapement level and considers additional herring as harvestable surplus. The second (Strategy II) requires a harvest proportional to estimated population size.

Strategy I was used in British Columbia from the start of the roe fishery in 1972 through the 1982 season. Desired spawning escapement was calculated as the amount of herring needed to deposit a quantity of spawn estimated to produce maximum numbers of larvae (Hourston 1980b). This caused very large harvests during years of strong recruitment. However, by cropping off all available surplus, no herring remained to balance or compensate for a declining abundance during years with poor recruitment. Biomass declines during these periods are exacerbated.

Strategy II is based on the philosophy that harvest schedule should parallel natural abundance cycles. This would allow a larger portion of each strong year class to remain unharvested to buffer population declines during periods of poor recruitment. As a safeguard, this strategy may include a minimum population biomass below which no harvest is allowed. One drawback to Strategy II is that during periods of extremely high abundance, spawning intensities may be high to increase egg mortality.

In jurisdictions using Strategy II, 20% of estimated biomass is generally used for setting quotas. In California, current management calls for a quota set at 20% of the biomass (spawning escapement plus catch) measured the previous year (PFMC 1982). Because estimated biomass has increased each year since surveys began in 1973 (Spratt 1981), harvest rates have only averaged about 12% of the available biomass. A fixed quota of 45 metric tons (t) in Oregon has resulted in a catch averaging 18% of the estimated biomass (J. Butler, ODFW, pers. comm.). In Washington, the maximum harvest is set as 20% of the average inseason point estimates (spawning escapement plus catch plus acoustic–trawl) if the biomass exceeds an 8165-t (9000 short ton) threshold (Trumble 1983). Alaskan management typically calls for a variable proportion ranging from 0 to 20%.

Limited Entry

The California Fish and Game Commission sets regulations that include limited entry for the herring fishery. Although new entries are allowed periodically, only new gillnet fishermen have been permitted in recent years. Purse-seine and lampara fishermen may trade their licenses for gillnet licenses. The 1981–82 fleet of 51 purse seiners and lampara boats and 410 gill nets (J. D. Spratt, CDFG, Monterey, CA, pers. comm.) results in serious overcrowding on the grounds, but management practices have kept harvest within the quotas.

No form of limited entry applies to treaty Indians in Washington, and their fleet generally increased each year until the fishery was curtailed in 1981. Nontreaty fishermen in Washington have been under legislated limited entry since 1973. Limited entry has only prevented an overcapitalized nontreaty fleet from becoming larger. The large roe fleet of

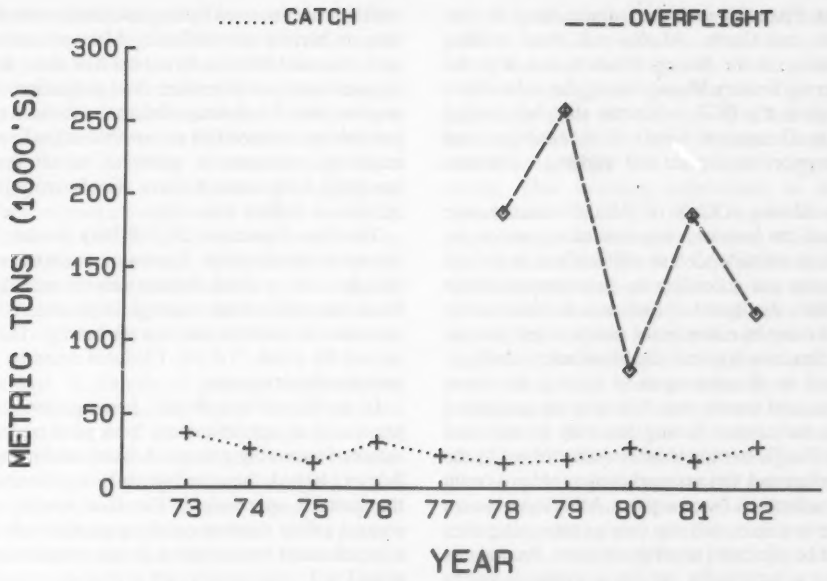

FIG. 8. Stock assessment and population trends for Pacific herring in the Bering Sea.

approximately 50 purse seines and 200 gill nets coupled with small quotas requires conservative management practices to prevent overharvest of the resource.

Limited entry has been established for various areas of the Gulf of Alaska. Some areas have fleets of 50–70 purse seines and 125–175 gill nets, many of which move between areas. Although fleet size is very large, catch has been maintained in a range compatible with resource size.

Alaska has not limited entry to herring fisheries in the Bering–Chukchi Sea, although fishermen must obtain a registration permit before fishing there. Two districts have been designated exclusive areas; herring fishermen choosing an exclusive area can fish nowhere else. The 1982 Bering Sea Togiak District roe fleet consisted of about 135 purse-seine and 200 gillnet vessels. This large catching capacity can overload available processing capacity. Approximately 300 more gillnet vessels fished in other parts of the Bering Sea. In spite of the large fleet, the harvest has been consistently at or below quotas.

Limited entry was introduced to the British Columbia roe herring fishery in 1974 to prevent an overcapitalized fleet from overexploiting the resource. These provisions did not apply to native Indians until 1977. Unfortunately, by the time limited entry took effect the fleet had grown to approximately 250 purse seines and 1300 gill nets, a fleet many times too large for efficient harvest of the resource. Overcrowding of both gear types on the fishing grounds led to implementation of further controls in 1981. An Area Licensing Program was set up in which each license holder was entitled to fish in only one of three designated areas on the coast.

Allocation Issues

No major herring stock on the Pacific coast of the United States and Canada has a harvestable surplus greater than the harvesting capacity of the fleet fishing on it. Demand for herring consistently exceeds quotas determined by management agencies. Allocation ultimately becomes a choice to provide fish to one or more user groups at the expense of other groups. Most commonly, herring are allocated by fishery type or product, for example, between roe, food, and bait fisheries, or between inshore and offshore fisheries. Within each fishery, allocation may be by gear type (gill net, purse seine, lampara) or by user group (Treaty Indian, non-Indian, or domestic–foreign). Management agencies normally allocate under legislative authority. Implementation of allocation requirements often involves setting quotas for vessels, gear types, or different users, establishing special (exclusive) fishing areas, or regulating fishing time.

California currently allocates most of its harvestable herring to roe fisheries (Spratt 1981). The largest roe fishery, in San Francisco Bay, has separate quotas for gillnet, purse-seine, and lampara gear users, as well as seasonal limits for individual purse-seine and lampara fishermen. The allocation has increased for gillnet fishermen because their catches have provided higher roe yields. Gillnet fishermen are divided into three groups, each fishing with different seasons.

Oregon is the only jurisdiction without specific herring allocation requirements. Small stocks, a restricted quota (about 45 tons/yr), and limited fishing effort have prevented fishing from exceeding resource capacity.

Specific fisheries in Washington are managed by area and gear restrictions, but no quotas for gear types are set within a fishery. Inefficient gear is used to harvest juvenile herring in areas of small populations to supply bait for recreational fishermen. Roe fishing, using purse seines and gill nets, occurs only in the area with the largest herring population. In 1974, U.S. District Court Judge George Boldt ruled that treaties signed in the 1850s gave certain Washington Indian tribes fishing rights to salmon and steelhead; subsequent hearings determined that the ruling also applied to herring (Trumble 1980). The Boldt decision allocates to the tribes up to 50% of the allowable harvest.

Allocation policies in Alaska are made by a politically

appointed Board of Fisheries and are administered by the Department of Fish and Game. Alaska will share herring allocation responsibility in the Bering–Chukchi Sea with the NPFMC once a Herring Fishery Management plan is in effect. NPFMC will allocate in the FCZ, while the state has control shoreward of 5.6 km (3 nautical miles). Both agencies have agreed on allocation priorities, but are still working to establish compatible policies.

In the southeast Alaska – Gulf of Alaska area, sac-roe fisheries take most of the harvest; only limited quantities are taken for food, bait, or subsistence use. Allocations in the roe fishery were originally set according to gear quotas within specific areas. In 1982, the Board of Fisheries divided fishing areas for exclusive fishing by either purse seines or gill nets. In the eastern Bering Sea, roe harvest also dominates landings. Gill nets are allowed in all areas open to fishing, but purse seines, beach seines, and trawls may fish only in designated districts. Herring in the eastern Bering Sea may be the most likely of any eastern Pacific herring to be underharvested by the inshore fishery. Weather and various marketing problems could prevent full inshore utilization in some years. MFCMA requires full utilization of the resource, and any surplus remaining after inshore fishing must be allocated to offshore users. Procedures to determine whether a harvestable surplus is available and to allocate such surplus have been very controversial and have not yet been defined.

At present, most of the annual quota in British Columbia is allocated to the roe fishery because this fishery provides highest economic returns to the most people. Provision is made for other uses of the overall quota, either through limited entry fisheries with fixed quotas or by special purpose fishing permits for such things as sport bait or aquarium and zoo food. The roe herring quota is further allocated between gear types: 55% seine, 45% gill net. This allocation is based on such factors as capital investment and numbers of fishermen employed in each sector.

In-Season Management of Roe Herring

Roe herring fishing is characteristically very intensive, with many more boats fishing than necessary for full utilization of the resource. In some areas, fishing may last only several hours or minutes. In other areas, the season may last for weeks or months. Variations in season length are determined by a combination of biological characteristics of herring stocks and the management goals of the responsible jurisdiction.

In British Columbia and most of Alaska, the timing and extent of roe herring openings are determined by prefishery assessments of the population. To maximize roe recovery, openings occur when herring are very near to spawning, and fishing takes place at a very high harvest rate. Setting openings is critical: too early an opening will cause harvest of herring insufficiently mature for high roe quality, and too late an opening will cause harvest of herring already spawning. Opening length is also important to ensure that harvests occur during the period of peak roe quality without exceeding the quota. Generally, exclusive gillnet fisheries may extend over several days. The higher catch rate of purse seines usually requires much shorter openings. In British Columbia, catching capacity of the seine fleet at a given location is sometimes so large that one successful set per boat would exceed the quota. This has led to openings as short as 15 min so that only part of the fleet will have an opportunity to complete a set.

By contrast, extended seasons in some jurisdictions occur with a preannounced fishing schedule, which is maintained as long as herring are available. Management agencies in areas with extended seasons do not open or close fisheries for quality requirements nor determine final utilization. Unlike very short seasons, which encourage fishermen to catch as many herring as possible or as much fish as possible regardless of quality (often requiring management agencies to set quality criteria for opening), long seasons allow fishermen to trade off quantity, quality, or fishing time.

The San Francisco Bay fishery is the best example of extended management. Spawning occurs from November into March; a 6- to 8-wk fishing season includes all or parts of December and extends through February. Actual season length depends on weather and spawn timing. The fishery operates around the clock, 5 d/wk. Closures occur by gear type as each gear reaches its quota.

In northern Puget Sound, herring spawn during April and May, with an approximately 3-wk peak period encompassing a series of spawning groups. A fixed roe fishing season is set for 3 d/wk, 10 h/d; the schedule shifts to a shorter fishing week as the quota is approached. The short weekly period is used to control a fleet that has catching capacity too large to maintain allocation and conservation quotas without severe time restrictions.

Most fishing in Alaska is managed with short seasons. However, in areas where runs are scattered or irregular, or where low fishing effort exists, a fixed quota and season may be set. Fishing may be continued until the quota is met. Similarly, in Oregon, where effort is low, fishing continues until a fixed quota is reached.

Discussion

Management of Pacific herring in the eastern Pacific Ocean is designed to balance the needs of the fishing industry with the protection of an historically overfished and naturally variable resource. Uncertainties in biological parameters have led to a general pattern of conservative management practices in which the resource receives the benefit of the doubt. However, actual management effectiveness has not been uniformly successful.

The single most successful practice has been restricting harvests to conservation quotas for various fisheries. Managers have tried to balance fishing time with available harvest; in most cases, this results in inefficient fishing practices, especially for roe fisheries. Large fleets with excess fishing capacity are controlled by reduced fishing time, exclusive fishing areas, individual boat quotas, and, in some cases, by not opening a fishery if control of the harvest cannot be maintained. Allocation quotas have been more difficult to achieve. Often, a large catch exceeding the quota for one gear or user group requires that competing groups take less than their allocations to maintain overall conservation requirements. Smaller fleets would allow more efficient operations. Recommendations to reduce roe herring fleets (Trumble 1977; Pearse 1982) have received some support from industry, but have been difficult to implement.

Canada has set an optimum spawning escapement, and population biomass exceeding this level was considered a harvestable surplus (Strategy I). All United States management agencies except ODFW use the management strategy of harvesting a set proportion of estimated herring biomass (Strategy II). A simulation model based on tradition yield-per-recruit analysis has been used to compare biomass, harvest

levels, and population stability resulting from various exploitation levels within these two strategies (PFMC 1982). In general, both strategies can maintain long-term stability of spawning escapement and protect against overharvest. However, Strategy I resulted in great variability in annual catch due to variability in recruitment: some years had extremely high catches, others had little or no harvest. Less variability in catch resulted from Strategy II: strong year classes carried over into subsequent years buffered effects of poor recruitment. A similar conclusion was reached by Walters et al. (1982) who recommended setting a proportionate exploitation rate for each Canadian stock. Stocker et al. (1983) further recommended that a 20% exploitation rate be used for harvest management. DFO subsequently set up a proportional harvest strategy in British Columbia following the 1982 season.

Direct measurement of abundance prior to or during the fishing season allows quotas to be based on actual stock condition. However, only two areas, Washington and the Bering Sea, currently set quotas from in-season stock assessment. Overflights used in the Bering Sea have many sources of errors and cannot provide statistically precise population estimates. However, this technique continues there as the primary stock assessment method because it has proven to be the most practical cost-effective method at the present time. The Bering Sea is the only area in the eastern Pacific where no abundance estimates are made from spawning ground surveys. Shallow depths and widespread herring have so far precluded use of hydroacoustics for population estimates just prior to spawning in the Bering Sea. Only Washington continues to use hydroacoustic assessment as a primary tool for in-season estimates, in combination with in-season estimates of spawning escapement and catch. Gulf of Alaska biologists, although involved in some of the pioneering work on hydroacoustic assessment of Pacific herring, have de-emphasized this technique. Changes in the distribution of prespawning herring have made hydroacoustic coverage unreliable. In British Columbia, low precision of abundance estimates obtained from roe herring fishermen echo sounder surveys led DFO to abandon this technique after the 1982 season. California and Oregon do not use in-season estimates of total abundance, although California anticipates developing a hydroacoustic program.

The tendency for reduced emphasis of in-season stock assessment has increased the need for accurate postseason stock assessment. In most cases, spawning escapement plus catch provides an estimate of total abundance. Few direct comparisons have been made to assess the accuracy of spawning escapement estimates. In the Washington roe fishery, spawning escapement, catch, and hydroacoustic data agreed very well from 1976 through 1980 but showed increasing differences in 1981 and 1982 (Trumble 1983). In southeast Alaska, preseason hydroacoustic estimates of roe herring from 1978 through 1980 consistently exceeded final spawning escapement plus catch, but hydroacoustic estimates may have included nonspawning herring (Blankenbeckler 1982).

Use of indirect assessment techniques, such as cohort analysis, to study Pacific herring populations may provide comparisons and allow greater insight to population dynamics. With only a 10-yr time series available for most roe fisheries, indirect techniques are just beginning to produce useful results. More detailed comparisons need to be completed of indirect and direct techniques as well as among different direct techniques. While this is pending, there will still be questions on the overall accuracy of stock assessment estimates.

In the past, minimizing the effects of natural fluctuations on yield, to stabilize yield, has often been poorly achieved. The fishing industry was frequently forced to prepare for a season without knowing the possible duration of the fishery, the magnitude of the harvest, or even if harvest would be allowed. As many jurisdictions have de-emphasized in-season biomass estimates, a trend has developed toward preseason quota setting. This increases information to industry on harvest expectation. California and Oregon have traditionally set preseason quotas because in-season estimates were not available. British Columbia and Gulf of Alaska managers will also be setting preseason quotas in future years.

Preseason quotas imply a degree of stability or predictive capacity that may not actually be achieved. Forecasting methods may be simple (based on herring abundance during the previous year or long-term mean abundance) or complex (age-specific projection of survivors from previous season added to estimated recruitment, or analytical models). Forecasted estimates are usually sufficiently reliable for management during periods of increasing or stable abundance if overestimates and underestimates average out. However, forecasted estimates can be misleading during periods of declining abundance. To prevent recruitment overfishing during such periods, forecasted quotas must be conservative.

Forecasting reliability could be improved with more accurate knowledge of population dynamics of exploited stocks. The most critical problem is the large fluctuation in recruitment, caused by variations in age of maturity and in year class strength. Thus far, research on juvenile herring has added little predictive capability to management activities. Such studies are difficult to conduct because data is needed on juvenile abundance, as well as biotic factors for extended time periods, in order to test and hypothesize on cause and effect relationships.

Another important problem has been separation of effects of natural fluctuations from effects of fishing. In the major fishing areas of British Columbia and Alaska, historical landings have substantially exceeded the current catches. British Columbia sustained a herring fishery of 100 000–200 000 t range for 20–30 yr before several years of poor recruitment and overfishing caused a sharp decline in yield (Hourston 1980a). Present landings range from 40 000 to 50 000 t. Similarly, Gulf of Alaska herring landings generally exceeded 50 000 t for 20–30 yr (Reid 1971), but are now less than 20 000 t. Bering Sea herring catches exceeded 100 000 t for several years during the 1960s, but subsequent landings have been between 20 000 and 40 000 t (NPFMC 1983). A 2000- to 4000-t winter (non-roe) harvest in Washington during the late 1950s and through 1970 had been reduced to several hundred metric tons by 1982 (Trumble 1983). Precipitous declines in herring abundance in both the Bering Sea and British Columbia have been attributed in part to overfishing. Current landings in the Gulf of Alaska, British Columbia, and some areas of Washington are consistently below the minimum harvest previously sustained for one to three decades.

Management agencies have established and maintained vigorous conservation requirements to protect the herring resource, in spite of the uncertainties and difficulties, and have attempted to use the best available scientific data as the basis for policies. However, uncertainties in herring stock assessments and harvest forecasts, difficulties in harvest allocations, and problems dealing with extreme, often unpredictable abundance fluctuations leave considerable room for improving management programs along the eastern North Pacific.

Acknowledgments

Compiling and summarizing the management practices for herring in the Northeast Pacific would not have been practical without the cooperation of the management agencies involved. The authors wish to thank Jerome Spratt (CDFG), Jerry Butler (ODFW), Dennis Blankenbeckler (ADGF), and Dr. Stephen Fried (ADFG) for providing information and for reviewing an early draft.

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Managing Herring Fisheries Under Uncertainty[1]

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The implications of the biological characteristics of the Atlantic herring (*Clupea harengus harengus*) on fishery management strategies are examined. Growth patterns and recruitment fluctuations limit opportunities to stabilize catches and stock biomasses without substantial loss of yield-per-recruit. The dynamics of herring stocks are much more dependent on recruitment than growth. Potential effectiveness of fishery management is also constrained by tendencies of herring populations to school, reducing self-regulatory possibilities by allowing catch rates to remain high when abundance is low, and to mix, complicating the estimation of catch-at-age and abundance indices. Given the vulnerability of herring to exploitation and the imprecision of abundance indices, achievement of relative stability of spawning stocks and catches requires adoption of fishing mortality rates near or below 0.2 in adult herring fisheries. Fisheries on immature herring reduce, and may destabilize, recruitment to spawning stocks and give lower yield-per-recruit than fisheries on mature herring although product prices may be higher. A simple stochastic model of the dynamics of an exploited herring population is examined. Analysis of this model demonstrated behaviour qualitatively similar to that observed in earlier studies of general production models subject to stochastic noise.

On examine les conséquences des caractéristiques biologiques du hareng de l'Atlantique (*Clupea harengus harengus*) sur les stratégies de gestion des pêches. Les régimes de croissance et les fluctuations du recrutement limitent les possibilités de stabiliser les prises et les biomasses des stocks sans perte importante du rendement par recrue. La dynamique des stocks de hareng dépend beaucoup plus du recrutement que de la croissance. L'efficacité potentielle de la gestion halieutique est aussi gênée, d'une part, par les tendances au regroupement en bancs des populations de hareng, ce qui réduit les possibilités d'auto-réglementation car les taux de capture restent élevés même quand l'abondance est faible, et, d'autre part, par les tendances au mélange de ces stocks, ce qui complique l'estimation des indices d'abondance et des prises selon l'âge. Étant donné la vulnérabilité du hareng à l'exploitation et l'imprécision des indices d'abondance, l'atteinte d'une stabilité relative des stocks reproducteurs et des prises exige d'établir des taux de mortalité par pêche à près de 0,2 ou moins pour la capture de harengs adultes. La pêche de harengs immatures réduit et peut déstabiliser le recrutement au sein des stocks reproducteurs et entraîner un plus faible rendement par recrue que la pêche de harengs adultes, quoique le prix des produits puisse être supérieur. On étudie un simple modèle stochastique d'une population exploitée de hareng. L'analyse de ce modèle a révélé un comportement qualitativement semblable à celui observé au cours d'études antérieures de modèles généraux de production soumis à un bruit stochastique.

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Following the collapse of a number of pelagic fisheries in the 1960's and early 1970's, particularly the herring fisheries of the North Sea and Norwegian Sea, the International Council for the Exploration of the Sea (ICES) convened a symposium in Aberdeen in 1978 to study the assessment and management of pelagic fish stocks. The editor, Alan Saville, summed up the conclusions of the symposium regarding why pelagic stocks are vulnerable to fishing, along the following lines (Saville 1980):

(1) There is strong evidence that catchability increases as stock size decreases.

(2) The ratio of production to stock biomass (P/B) is probably lower in most pelagic fish than in most demersal fish.

(3) It seems likely that the left-hand limb of the stock–recruitment curve in demersal species is steeper than in pelagic ones, permitting a higher exploitation rate without reduction of recruitment.

(4) It is possible that predatory mortality increases when stock size decreases, analogously to catchability, in pelagic fish.

Attention was also drawn to general agreement that maximum yield-per-recruit is an untenable management criterion due to overestimation of current stock size. The need for fisheries-independent stock abundance estimates was noted.

The present paper begins with an analysis of biological factors important to the management of herring fisheries including the unresolved problems associated with managing mixed stock fisheries. This analysis leads to the formulation of a

[1]This paper was presented at the International Symposium on the Biological Characteristics of Herring and Their Implication for Management, convened at Nanaimo, B.C., June 20–22, 1983, commemorating the 75th anniversary of the Pacific Biological Station.

simple stochastic model of a fished herring stock permitting rough quantification of the influence of different factors on yield, spawning stock biomass, and stability of stock and catches.

Material and Methods

No new data are presented here. Estimates of biological parameters, year-class sizes, and partial recruitment have been drawn from the literature with a view to establishing an empirical basis for subsequent modelling.

Biological Parameters

Natural Mortality

An instantaneous annual natural mortality rate (M) of 0.2 is normally assumed in analysis of herring population dynamics in the North Atlantic. Predation studies and theoretical analysis (e.g. Anderson and Ursin 1977; Ursin 1982) indicate that higher rates of predation mortality are likely to occur on herring less than 2 yr old; but, in the absence of epidemic phenomena, such as mass mortality of herring in the Northwest Atlantic Fisheries Organization (NAFO) Division 4T in 1954–56 (Sinderman 1958), natural mortality rates on herring older than 2 yr are indistinguishable from a constant value.

Since the author is not aware of any positive evidence, the fourth, tentative, conclusion of the Aberdeen Symposium is considered speculative. The availability of herring more than 10 yr old for several years in the declining Newfoundland fisheries (Moores et al. 1981) suggests that M may be less than 0.2 in this area. A value of $M = 0.2$ is adopted for further calculations with some attention paid to the implications on yield-per-recruit calculations of $M = 0.1$ and $M = 0.3$.

Growth

Beverton (1963) and, subsequently, Anthony and Waring (1980) tabulated von Bertalanffy growth parameters for many Atlantic herring (*Clupea harengus harengus*) stocks. All showed rapid growth in the first years of life, slowing markedly at the onset of maturity, normally about age 4.

Although there is some evidence of density-dependent growth of young herring, the literature is contradictory regarding density-dependent growth of mature herring (Sinclair et al. 1982b). Any such density dependence must be weak, since even a doubling of growth rates would, in most cases, imply less than 20% annual growth in weight.

Published estimates of the Brody coefficient K vary from 0.17 to 0.60 (for Baltic herring). For Canadian Atlantic herring populations and Atlanto–Scandian herring, K was estimated to be between 0.17 and 0.30. In the North Sea and the Irish Sea the range was 0.2–0.43. Anthony and Waring (1980) estimated K for the Georges Bank population at 0.35–0.36. In all cases, 50% maturity occurs at lengths near 80% of the asymptotic length L_∞.

The following table shows the increments of natural logarithms of weight at age in successive years following the achievement of 80% of L_∞ for a range of values of K using the von Bertalanffy model:

	K					
Years	0.15	0.2	0.25	0.3	0.35	0.4
0	0.103	0.133	0.161	0.188	0.214	0.238
1	0.086	0.105	0.12	0.132	0.142	0.149
2	0.072	0.083	0.09	0.094	0.096	0.096
3	0.06	0.066	0.068	0.068	0.066	0.063
4	0.051	0.053	0.052	0.049	0.046	0.041
5	0.043	0.043	0.04	0.036	0.032	0.027
6	0.037	0.035	0.031	0.026	0.022	0.018
7	0.031	0.028	0.024	0.019	0.016	0.012
8	0.027	0.023	0.018	0.014	0.011	0.008
9	0.023	0.019	0.014	0.011	0.008	0.005

Thus, growth rates for Atlantic herring slow markedly following maturity and are then typically less than the assumed natural mortality rate of 0.2. The average growth rate for a mature herring population is 0.1 ± 0.05 unless the age structure is very extreme. Further calculations for example stocks use this result or observed mean weights-at-age.

Yield-Per-Recruit

Figure 1 illustrates the cumulative effects of growth and natural mortality on a single year-class of herring in southwest Nova Scotia. Figure 1b shows that when the natural mortality rate is 0.2, unexploited biomass is maximal at age 5 and declines steadily thereafter. Mean weight-at-age are averaged data taken from CAFSAC Res. Doc. 82/36. The biomass is within 20% of the maximum for four age-classes. If $M = 0.1$, a year-class can be caught over a wider range of ages without loss of yield (Fig. 1a), while if $M = 0.3$, yield-per-recruit drops rapidly beyond age 6. Thus, provided the natural mortality rate does not exceed 0.2 by much, yield from a strong year-class can be spread over several successive years with little loss in average catch and considerable stabilization of catch and biomass levels relative to what would occur with a high fishing mortality on the optimal age group. This possibility is examined further below, in the context of recruitment fluctuations.

In the case of southwest Nova Scotia herring, which is considered later, the theoretical maximum yield-per-recruit aged 1, associated with the above-mentioned mean weights and harvesting the entire standing stock for a year-class at the age when its biomass is greatest, is 102 g so that, given the historical average recruitment of 2.21×10^9 at age 1 of CAFSAC Res. Doc. 82/36, a theoretical maximum average catch of 225 000 t could be taken from the stock if there were no stock–recruitment relation. This is twice the average catch over the period for which recruitment was averaged. The difference is largely due to high catches at ages 1–3, especially in the purse-seine meal fishery for much of the late 1960's and early 1970's.

Recruitment

Year-class sizes from published VPAs were examined to determine their variability. Since the VPA estimates are not exact and the time series are relatively short, these represent rough estimates of "true" values. The coefficients of variations

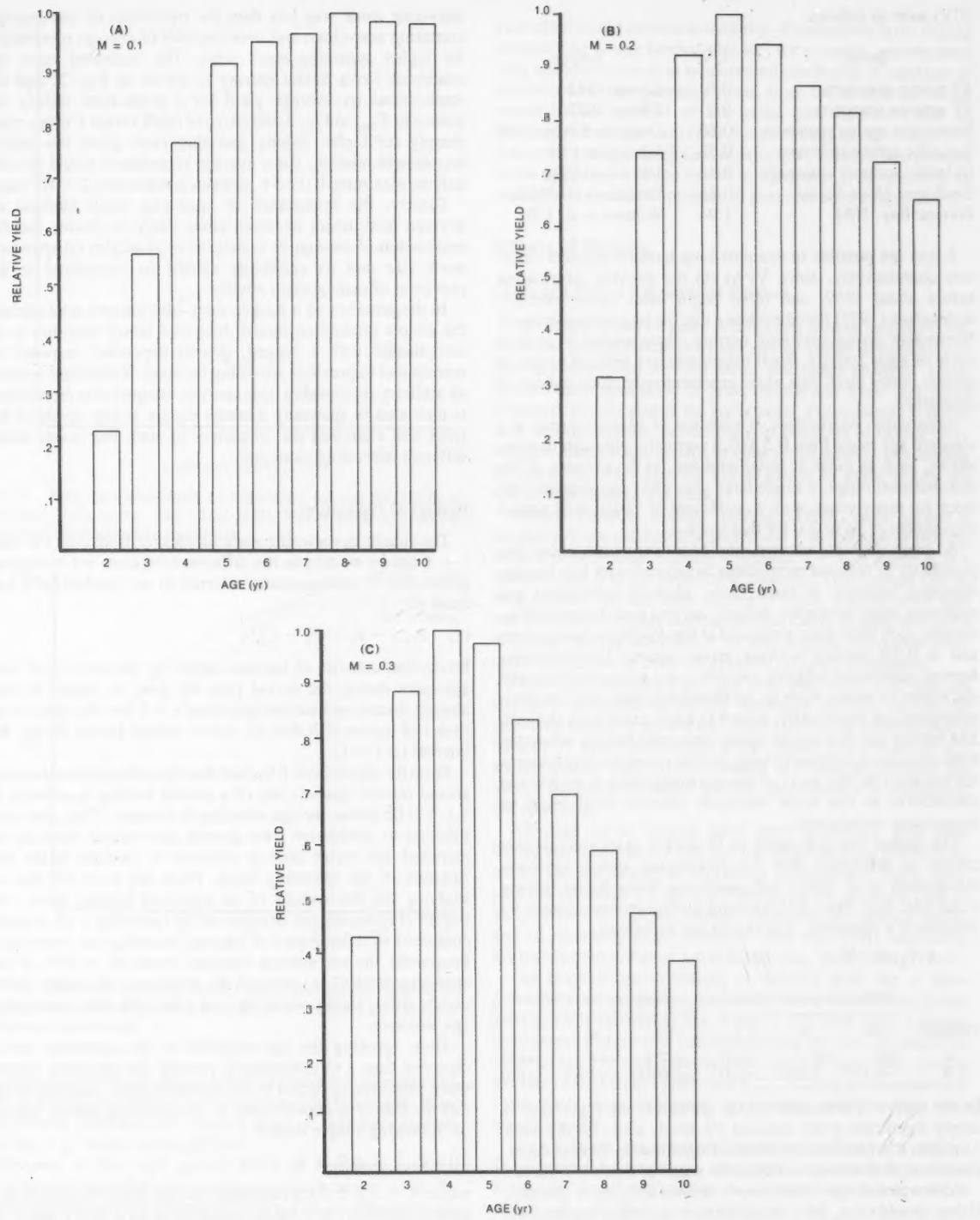

FIG. 1. Southwest Nova Scotia herring growth rates exceed 0.2 until age 5. The potential yield-per-recruit is shown for three values of *M*: (A) 0.1, (B) 0.2, and (C) 0.3. It is assumed that all fish would be harvested at a single age.

(CV) were as follows:

Stock	CV	Source
4T spring spawners	0.9	Cleary 1982
4T autumn spawners	0.7	Cleary 1982
Norwegian spring spawners	0.65	Dragesund et al. 1980
Icelandic spring spawners	0.55	Jakobsson 1980
Icelandic summer spawners	0.48	Jakobsson 1980
Southwest Nova Scotia	0.86	Sinclair et al. 1982a
Fortune Bay, Nfld.	1.94	Winters et al. 1985

It was not possible to examine long-term recruitment variation quantitatively, since VPAs do not provide information before about 1950, and often begin much more recently. Kolesnikov (1977) found evidence that the long-term catches of Norwegian spring spawning herring corresponded to an 8-yr cycle of solar activity. Such hypotheses are difficult to test at present, since catch data alone represent only crude indices of abundance.

Apparently, coefficients of variation of year-class size at a standard age range from 0.5 to 0.9 normally, although in some stocks, such as those at Newfoundland, at the extreme of the distributional range, a single large year-class can dominate the stock for many years, with a coefficient of variation of annual recruitment of up to 2.0 for that stock.

A great deal of concern has been expressed about the possibility of reduced recruitment associated with low herring spawning biomass. In many cases, plots of recruitment and spawning stock biomasses strongly suggest such a relationship. Several such plots were presented at the Aberdeen Symposium and in ICES herring working group reports. Unfortunately, herring recruitment is highly variable at any given stock size and the scatter of points leads to parameter estimates that are often nonsignificant statistically, except in a few cases such as North Sea herring and Norwegian spring-spawning herring where the time series is exceptionally long. Another confounding factor is the tendency for the years of low spawning stock to be few and consecutive so that some multiyear external trend could be suppressing recruitment.

The author has attempted to fit Ricker stock–recruitment curves to published data for Norwegian spring spawners (Dragesund et al. 1980) and southwest Nova Scotia herring (CAFSAC Res. Doc. 82/36) using nonlinear least squares by Marquardt's algorithm. The results are as follows:

$$R = aBe^{-bB}$$

	Norwegian spring spawners			Southwest Nova Scotia		
Parameter	Est.	SE	t	Est.	SE	t
a	284	125	2.27	1.272	46.5	0.027
b	−0.157	0.0692	−2.27	−0.00183	0.0913	−0.020

In the case of Norwegian spring spawners, the regression is barely significant at the nominal 5% level, while for the other example, it is not close to statistical significance. In both cases, there is no evident way to define the shape of a possible curve.

Although such curves are poorly defined and may be illusory, if they should exist, there would be very important implications on herring management, since continued strong recruitment is so vital and taking catches near the maximum yield-per-recruit greatly reduces the average spawning stock biomass with inevitable associated instability. In the case of southwest Nova Scotia herring, observed recruitment from VPA, when the spawning stock was less than the equivalent of one average recruiting year-class, was only one-half of average recruitment for higher spawning stock sizes. The estimated curve for southwest Nova Scotia herring is shown in Fig. 2, and the implications on average yield for a purse-seine fishery are plotted to F_{max} in Fig. 3; the curve of catch versus F drops more sharply for higher fishing mortality rates given the stock–recruitment relation, since average recruitment would be only half the maximum if the 5+ biomass is reduced to 2×10^5 tons.

Clearly, the importance of spawning stock biomass on average recruitment deserves close study in future, and the implication of alternative management strategies on spawning stock size and its variability should be considered in the provision of management advice.

In the presence of a Ricker stock–recruitment relationship, the simple production model described below becomes more complicated with a lagged, density-dependent response of recruitment to previous spawning biomass. Rather than assume an arbitrary relationship, this analysis assumes that recruitment is unrelated to spawning biomass except at low levels of the latter and examines the frequency of such low levels under different harvesting strategies.

Biological Production

The change in spawning stock biomass B_t from time t to time $t + 1$ can be written as the difference between net biological production P_t (subsequently referred to as "production") and catch C_t:

$$(1) \quad B_{t+1} - B_t = P_t - C_t.$$

Production consists of biomass added by recruitment of new spawners during the period plus the gain in weight by fish already mature and surviving to time $t + 1$ less the biomass at time t of mature fish that die due to natural causes during the interval $(t, t + 1)$.

From the above table it is clear that the average instantaneous annual relative growth rate of a mature herring population is 0.1 ± 0.05 unless the age structure is extreme. Thus, the contribution to production from growth and natural mortality of recruited fish varies little in response to changes in the age structure of the spawning stock. From the point of view of studying the fluctuations of an exploited herring stock, the impact of changing age structure of the spawning stock is small compared with the impact of varying recruiting year-class size. Frequently the recruitment biomass varies by ±50% of the spawning stock (2 SE) whereas the production per tonne of the mature fish typically varies by less than ±5% due to changing age structure.

Thus, ignoring the age structure of the spawning stock, choosing time t to immediately precede the spawning season when year-classes recruit to the spawning stock, and assuming that the fishery is concentrated in the spawning season lead to the following simple model:

$$(2) \quad B_{t+1} = a(B_t + R_t - C_t)$$

where $a = 0.9 \pm 0.05$ represents the net effect of growth and natural mortality, R_t is the recruiting biomass in year t, and C_t is the catch in year t. This model closely approximates the dynamics of production and is more appropriate than the age-structured projections assuming constant recruitment commonly used to forecast stock sizes and catches when questions of stability are to be considered.

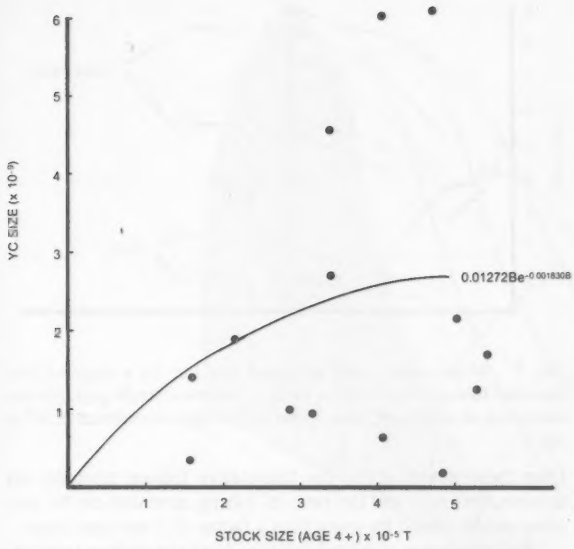

FIG. 2. Year-class abundance and spawning stock size for herring at southwest Nova Scotia. The fitting of the Ricker stock–recruitment curve was not statistically significant.

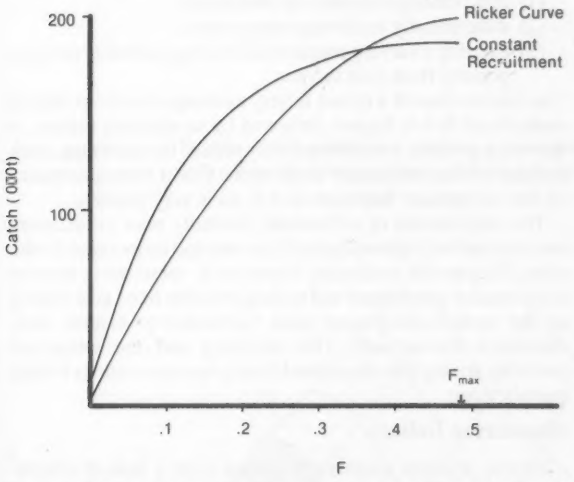

FIG. 3. Effect of assuming Ricker stock–recruitment relation of Fig. 3 on calculated mean yield for a purse-seine fishery for herring at southwest Nova Scotia.

A herring fishery can be considered to have two components, one on mature fish and one on immature fish. Frequently these components correspond to distinct gears or seasons with little overlap, e.g. weirs versus gill nets.

Because of the high growth rates of immature herring, catching herring before they mature results in loss of yield, the losses being greater for younger fish (e.g. Fig. 1). The effect of a young herring fishery on the dynamics of the spawning stock depends on how the fishing mortality rate varies from year to year. Exerting a constant fishing mortality rate on young herring results in reduced recruitment to the spawning stock but the same coefficient of variation of recruitment as would occur with no young herring fishery, since a fixed proportion of each year-class would survive to maturity. Fluctuations in the fishing mortality on young herring that are, for example, uncorrelated with abundance result in an increased coefficient of variation of recruitment to the spawning stock, since the number surviving would be the product of the initial year-class size and an uncorrelated random survival factor. Thus, maintenance of a fishery on young herring can, in principle, be taken into account in the application of the model in equation (2) by choosing an appropriate stochastic process to generate recruitment, R_t.

Effects of Fishing

Gears and Partial Recruitment Patterns

The combination of gears in a herring fishery influences the pattern of fishing mortality by age and the ability of fishermen to find fish when their distribution or abundance changes. There are two main categories of gear, mobile and fixed. The most important mobile gear is the purse seine. Purse seiners actively seek herring schools, permitting concentration of fishing mortality on selected age groups in view of the tendency of herring to school by size. Herring are available to purse seines for extended periods of the year.

Several authors, notably Ulltang (1980), have shown a tendency of the catchability coefficient q to increase as herring stock size decreases. Ulltang suggested $q = K/B$ where K is a constant and B is the exploitable biomass. This implies that as long as there are sufficient herring to catch, a purse-seine fleet can maintain a roughly constant annual catch, in spite of rapidly declining herring abundance. It also implies that purse-seine catch rates provide little information on stock abundance.

Fixed gear includes traps, gill nets, and weirs. Gill nets are normally deployed on herring spawning grounds during the spawning season of up to 6 wk. Mesh size can be adjusted over a number of years to strongly affect partial recruitment at age among mature fish. Gillnet catches in Canadian fisheries are mainly landed in two short periods, associated with spring and fall spawning.

Although purse seiners have been associated with high fishing mortality rates, extensive use of gill nets can also rapidly reduce the abundance of recruiting year-classes. Catch composition estimates for herring fisheries in the southern Gulf of St. Lawrence (L. Cleary, unpubl. data) indicate virtual elimination of recruiting year-classes in 1980 and 1981, suggesting fishing mortality rates of 1.0 or higher due, mainly, to gill nets.

The implications of fishing exclusively with one of three gears, purse seine, gill net, and weir, on southwest Nova Scotia herring are illustrated in Fig. 4 and 5. For each gear, a partial recruitment pattern was calculated using the ratio of historical catch-at-age for that gear to total catch-at-age times fishing mortality at age from a published VPA, scaling to a maximum of 1 for each year, averaging over years, and rescaling to a maximum of 1.

In each figure, the mean and the mean less 1 SD were plotted. The standard deviation was calculated assuming independent, identically distributed annual recruitment at age 1 with a mean of 10^9 and a coefficient of variation of 0.86.

The weir fishery has much lower yield-per-recruit than the other two, due to its dependence on age 1–3 fish. Given a regime of constant fishing mortality, the purse-seine fishery gives a higher, and more stable, catch but a lower population and spawning stock biomass at moderate fishing mortality rates than the gillnet fishery.

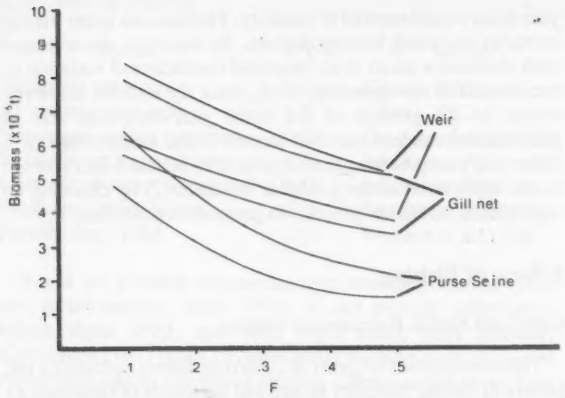

FIG. 4. Mean spawning stock biomass and mean less 1 SD for a range of fully recruited fishing mortality rates for three hypothetical single gear fisheries on herring at southwest Nova Scotia and average recruitment of 10^9 at age 1.

Possibilities to spread out the contributions of a strong year-class to the spawning stock and to catches in a purse-seine fishery are illustrated in Fig. 6 and 7. As the fishing mortality rate increases, the spawning stock and catches become increasingly dominated by herring aged 3–5. At fishing mortality rates below 0.2, a strong year-class can make a significant contribution at age 8 and beyond.

Mixed Fisheries

Herring fisheries are frequently composed of contributions from distinct spawning grounds. This is very evident in the North Sea, the Bay of Fundy, and the Gulf of St. Lawrence, and represents a major obstacle to assessing the herring population fished in winter off Cape Breton Island, Nova Scotia.

Typically, the origin of individual fish in mixed herring fisheries is difficult, or practically impossible, to determine. This can lead to down-playing of the implications of mixing of stocks on fishery management. For example, the 1980 Alaska Herring Symposium concluded (Melteff and Wespestad 1980, p. 265) "The general consensus among the biologists present was that mixed stock fishing per se could not be viewed as detrimental to individual stocks or the well-being of a group of stocks."

In view of the numerous possible ways in which component stocks or races could mix in exploited populations, the composition of herring catches in NAFO Division 4T + 3Pn is extremely revealing. Its value is to show, at least roughly, what has happened in one case when the composition of catches has been estimated. Figure 8 (redrawn from Cleary 1982) shows how the estimated composition of the total catch, and of various components, based on assignment to spring and fall spawning components via maturity stages, has varied historically. Some of the variation observed is undoubtedly due to the scarcity of samples, particularly before 1973, but it is clear that the degree of mixing has varied greatly from year to year.

G. H. Winters (pers. comm.) has provided the author with approximate estimates of fishing mortality rates for spring and fall spawner herring in Division 4T − 3Pn:

Year	1969	1970	1971	1972	1973	1974	1975
Spring spawners 3+	0.24	0.35	0.20	0.08	0.13	0.10	0.14
Autumn spawners 3+	0.21	0.31	0.46	0.27	0.11	0.09	0.09

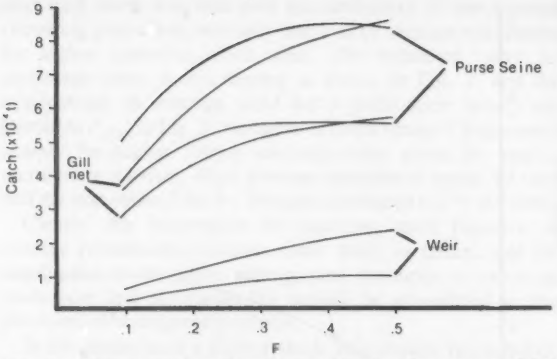

FIG. 5. Mean annual catch and mean less 1 SD for a range of fully recruited fishing mortalities for three hypothetical single gear fisheries on herring at southwest Nova Scotia and average recruitment of 10^9 at age 1.

Over these seven years, the cumulative fishing mortality on autumn spawners and the ratio of fishing mortality on the two components varied by more than a factor of 2 between years.

The importance of mixed fisheries has been underestimated, in the author's view, due to lack of reliable information on the composition of mixed catches. Mixed fisheries complicate optimal management of component stocks or races by

(1) confounding estimates of abundance;
(2) differentially exploiting components;
(3) exerting a varying proportion of fishing mortality on components from year to year.

The combination of a mixed fishery exerting an average fishing mortality of 0.4 or higher, followed by an efficient fishery on spawning grounds, could drastically reduce the spawning stock biomass of one component stock in one year if fishing mortality on this component fluctuates to 0.8, as is very possible.

The implications of differential mortality rates on different races are reduced spawning stock for one and an increase for the other. This would invoke any latent stock–recruitment relation in the weaker component and make a possible fixed gear fishery on the weaker component more vulnerable to natural stock abundance fluctuations. This tendency and the estimation problems arising from the mixed fishery increase with its fishing mortality rate.

Abundance Indices

Herring resource assessment suffers from a lack of reliable abundance indices. In practice, much of the discussion of herring assessment working groups has related to evaluating proposed indices. To illustrate the nature of the problem, the author regressed indices of abundance as a function of the corresponding quantity calculated from VPA (Cleary 1981).

The table below gives the residual standard error of the regression divided by the median value of the dependent variable. This is a rough indication of the precision (CV) of these indices and ignores large potential biases:

Index	Independent variable	SE/median
Fall PS catch/set	2 + biomass	0.33
GN lb/net day	2 + biomass	0.41
GN lb/net day	5 + biomass	0.70
Mag. Is. trap t/trap	2 + biomass	0.57
Mag. Is. trap t/trap	5 + biomass	0.80
Research vessel Nos./tow	5 + numbers	0.90

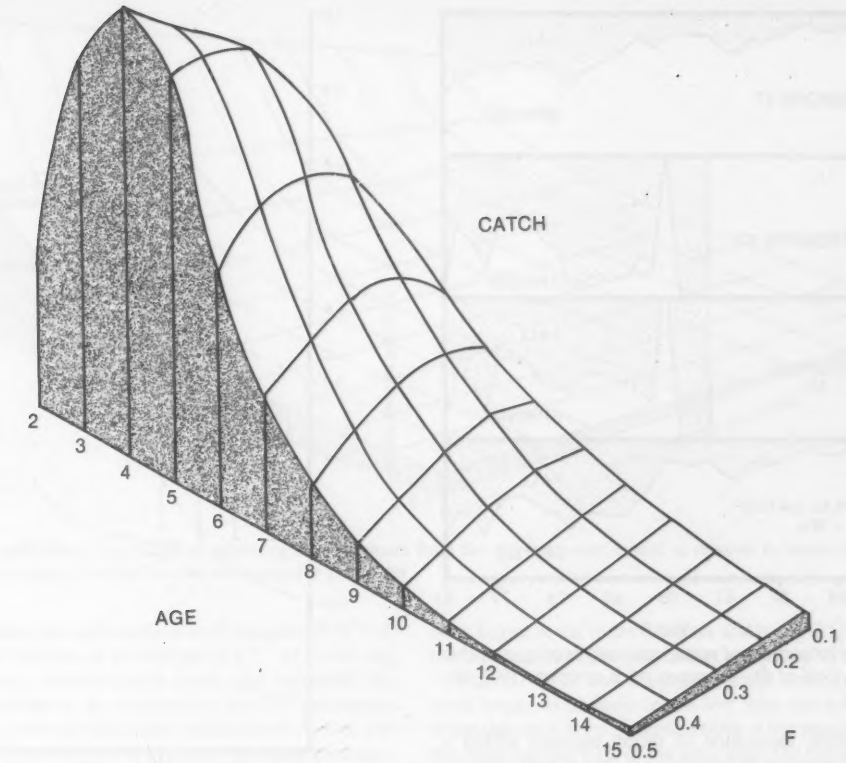

FIG. 6. Catch-at-age for a single year-class of herring exploited by a hypothetical purse-seine fishery with a constant fishing mortality rate (on fully recruited ages).

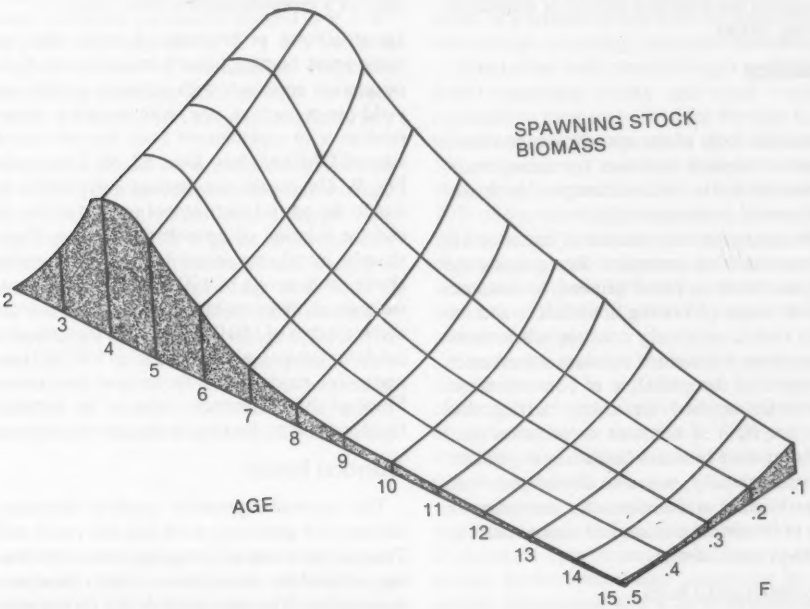

FIG. 7. Contribution of a single year-class of herring to spawning stock size at various ages under a hypothetical fishery.

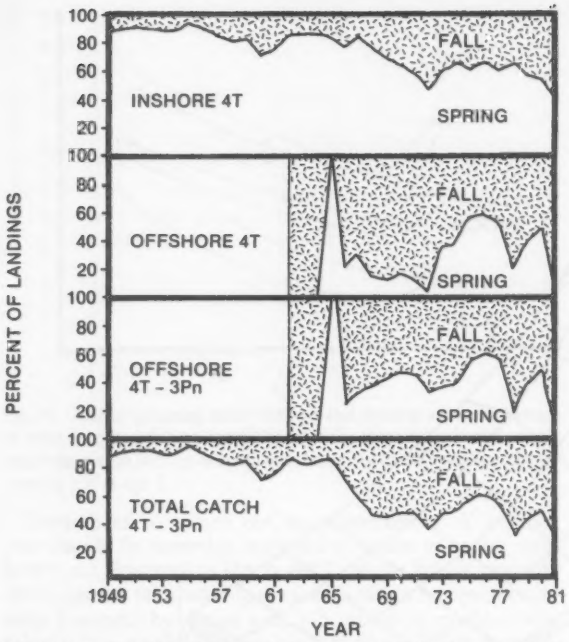

FIG. 8. Estimated proportions of spring-spawning herring in catches from the Southern Gulf of St. Lawrence stock complex (1949–81) (from Cleary 1982).

With such indices, estimation of recent biomass within a factor of two may seem an ambitious goal. In the next section, means of coping with this problem are outlined.

With the exception of the wild 1981 value, the herring larval survey at southwest Nova Scotia has been remarkably consistent with VPA estimates of the spawning biomass usually within 10%. This example suggests that effective indices of abundance may be found for herring stocks.

Mathematical Modelling

Assumptions

The simple mathematical form of the autoregressive model permits the calculation of explicit formulas for mean catch, variance of catch, mean biomass, and variance of biomass. These formulas are presented in the appendix.

The behaviour of the autoregressive model of equation (2) was examined with three catching strategies. Recognizing the tendency of mobile gear, such as purse seiners, to maintain catch levels over a wide range of herring abundance, and the tendency for quotas to remain relatively constant when abundance estimates are uncertain, a system of constant annual catch was considered. Recognizing the guideline of constant target fishing mortality currently applied for many herring and groundfish resources, a system of constant exploitation rate, defined as the fraction of mature biomass (including the current year's recruits) harvested annually, was also considered, with and without errors of estimation of abundance for the setting of quotas. The behaviour of the model was studied mathematically and by a series of 1000-yr simulations.

Comparison with Age-Structured Model

The behaviour of the autoregressive model which does not consider the age structure of the stock was compared with

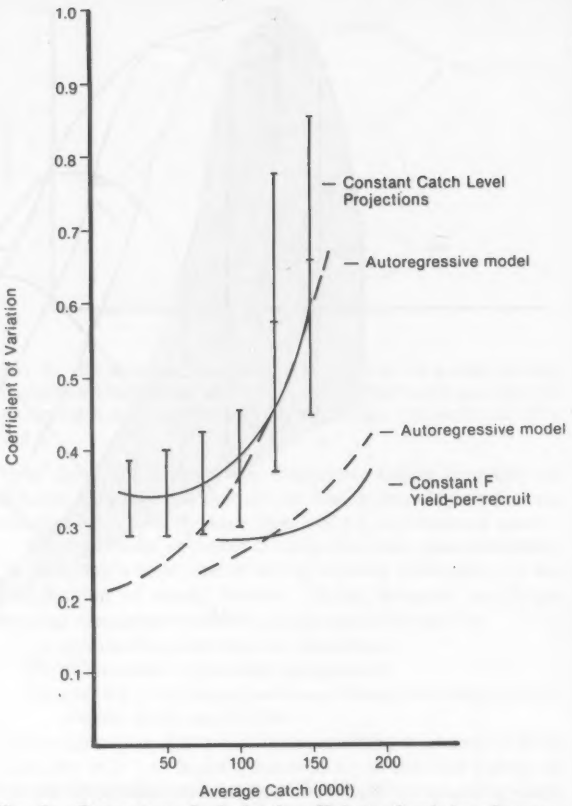

FIG. 9. Comparison of calculated coefficients of variation of spawning stock biomass for southwest Nova Scotia herring from the simple autoregressive model and age-structured simulations and yield calculations for a hypothetical purse-seine fishery.

age-structured projections of stock size and catch for the purse-seine herring fishery in southwest Nova Scotia, using a simulation approach with constant catches and calculations of yield-per-recruit at age with varying recruitment drawn at random with replacement from the set of estimated year-class sizes of CAFSAC Res. Doc. 82/36. The results are illustrated in Fig. 9. The results are qualitatively similar but differ in detail due to the partial recruitment pattern of the purse-seine fishery and the relation of growth rate to age. Both models indicate sharply increasing instability for the constant catch strategy above catch levels of 100 000 t. The constant fishing mortality strategy is more stable but also shows increasing instability above catches of 150 000 tons. The theoretical maximum average catch for the purse-seine model is 187 000 tons, while the autoregressive model has a theoretical maximum of 225 000 tons. Much of this difference is due to the harvesting of immature, rapidly growing herring in the purse-seine model.

Analytical Results

The appendix presents explicit formulas for means and variances of spawning stock size and catch and related qualities. These apply to the autoregressive model when it is stationary in the probabilistic sense of reaching a time invariant probability distribution. The derivation of the formulas is straightforward. For more information regarding autoregressive models, see Cox and Miller (1965). The formulas are illustrated in Fig. 10–13.

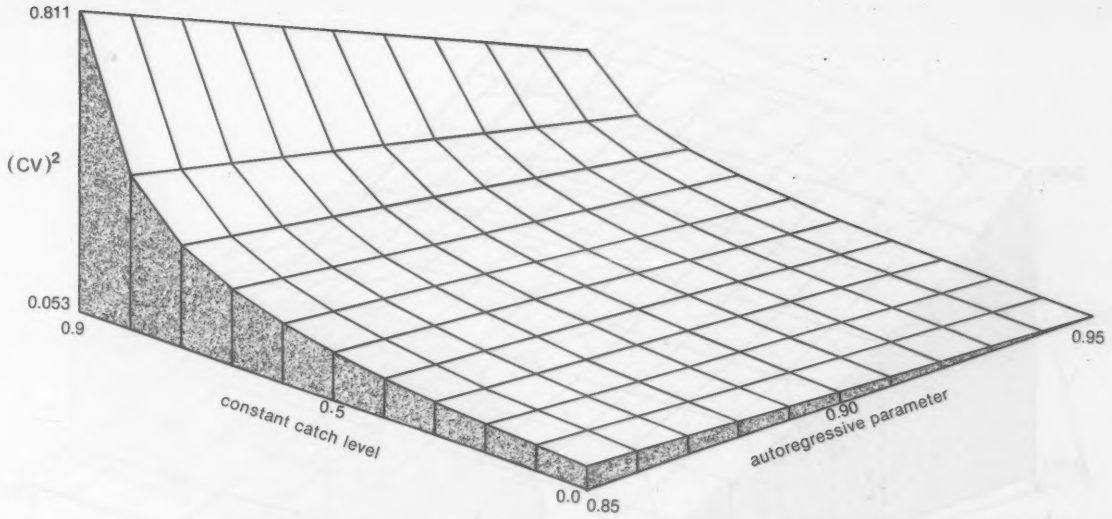

FIG. 10. Squared coefficient of variation of spawning stock biomass from the autoregressive model in relation to levels of constant annual exploitation rate and a range of values for the autoregressive parameter.

Figure 10 shows the squared coefficient of variation (CV^2) of the spawning stock biomass as a multiple of CV^2 of recruiting biomass for differing constant catch levels and values of the autoregressive parameter a. As a increases, the CV^2 decreases. Variability increases sharply for catch levels above 70% of the theoretical maximum given by the average recruiting biomass. Figure 11 is similar to Fig. 10, but with a constant exploitation rate.

Figure 12 shows the implications of estimation variance on stability of the spawning stock biomass when a target exploitation rate is applied to an estimated spawning stock biomass with $a = 0.9$. The estimator's relative variance is defined as $V \div R^2$ and the CV^2 is expressed as a multiple of $\Sigma \div R^2$, i.e. as a multiple of the relative variance of recruitment. Estimator variance had little impact on spawning stock stability for target exploitation rates below $\gamma = 0.25$ but is a significant factor at $\gamma = 0.4$ and above.

Figure 13 illustrates the potential for increased catches with comparable stability when a constant exploitation rate strategy is adopted instead of a constant catch level strategy. The difference in average annual catch for a given target constant exploitation rate and the corresponding constant catch leading to the same coefficient of variation of spawning stock size is plotted. The vertical scale is in units of theoretical maximum catch (1 = 100%). Significant increases in average yield can be achieved with equivalent CV^2 of spawning stock biomass for a constant exploitation rate up to 0.25, even when estimators of biomass are as variable as annual recruitment. At higher exploitation rates, estimator variance becomes an important limiting factor.

Simulation Results

The behaviour of the autoregressive model was further investigated by a series of 1000-yr simulations with differing parameters ($a = 0.85, 0.9, 0.95$) and recruitment distributions corresponding to herring at southwest Nova Scotia, Norwegian spring spawners, and Fortune Bay, Newfoundland. All simulations began at the mean biomass and had a random sequence of recruitment drawn from the observed (from VPA) distributions.

With $a = 0.9$ and a constant catch strategy, the spawning stock began to frequent levels less than one average year-class when the catch level exceeded 60% of the maximum and was in this region about 10% of the time when the catch was 75% of the maximum, in the case of southwest Nova Scotia herring and Norwegian spring spawners.

The corresponding thresholds for the more variable Fortune Bay case were 40 and 50% of theoretical maximum catch, respectively. Closure of herring fisheries, due to low spawning stock, is a serious option with the spawning stock below one or two average recruiting year-class biomasses.

Simulations with constant target exploitation rate led to more stable spawning stocks and more variable catches. With exploitation rates up to 0.10 for Fortune Bay herring and 0.2 in the other cases, the spawning stock size rarely (less than 3 and 1%, respectively) was less than one average recruiting year-class, R. An exploitation rate of 0.2 gives average catches about 70% of the theoretical maximum. At exploitation rates of 0.3, the fraction of years with spawning stocks below R was 5–40%, depending on recruitment distribution. The average catch increased by about 10% of the maximum. Beyond an exploitation rate of 0.3 the fraction of years at low spawning biomass increased sharply.

Sensitivity runs for the southwest Nova Scotia recruitment distribution and $a = 0.85$ and 0.95 showed lower average catches (10% less at exploitation rate 0.2) and higher variability of spawning stock size at $a = 0.85$ and corresponding lower variability and higher catches (13% more at exploitation rate 0.2) for $a = 0.95$.

In all cases, at exploitation rates of up to 0.30, the most important result of increasing estimation error in the constant exploitation rate strategy was larger annual adjustments to quotas. In the intermediate, southwest Nova Scotia case, with perfect information and a 20% exploitation rate, the average percent change in annual catch was 22%, rising to 33% at an exploitation rate of 0.3 and 36% at an exploitation rate of 0.2

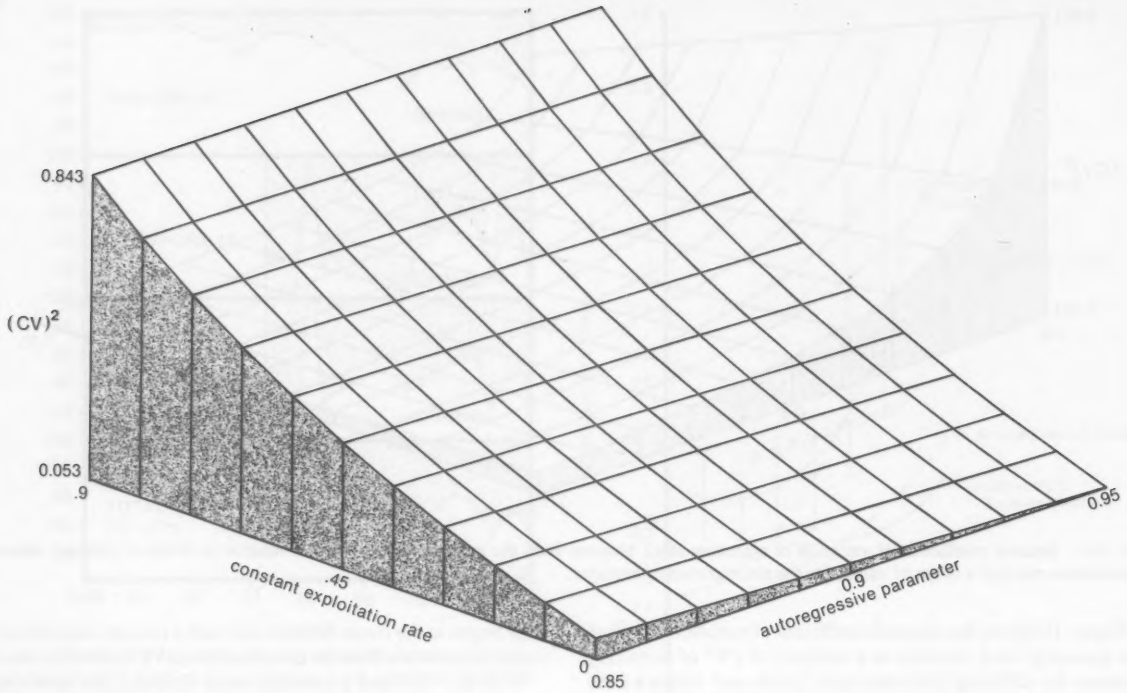

FIG. 11. Squared coefficient of variation of spawning stock biomass from the autoregressive model in relation to levels of constant annual catch and a range of values for the autoregressive parameter.

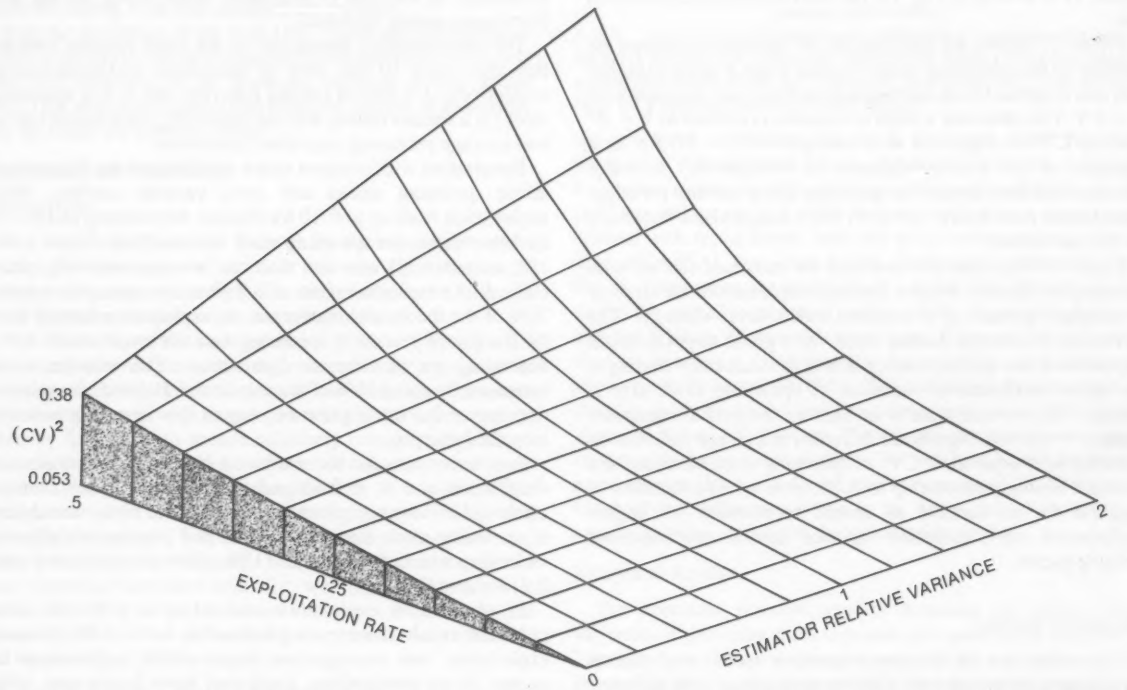

FIG. 12. Squared coefficient of variation of spawning stock biomass from the autoregressive model in relation to target constant exploitation rates applied to biomass estimates of varying precision. Estimator relative variance is defined as estimator variance divided by squared coefficient of variation of recruitment.

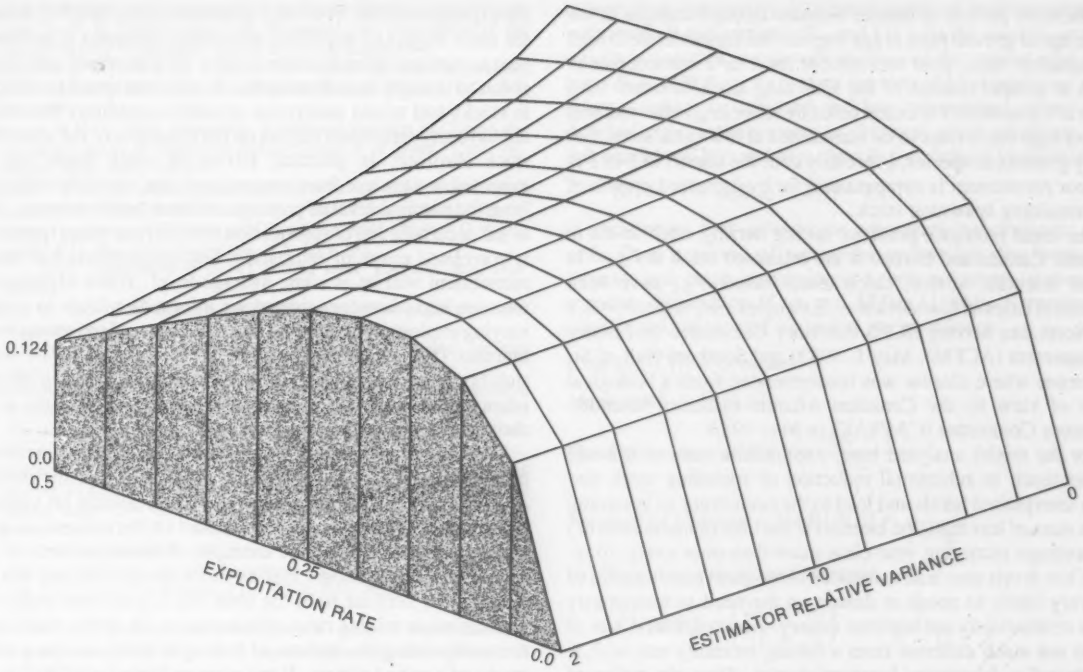

FIG. 13. Application of a constant target exploitation rate allows higher catches to be taken on the average than a constant annual catch strategy for the same coefficient of variation of spawning stock size. The difference in average annual catches as a fraction of mean annual recruitment biomass (z-axis) is shown in relation to exploitation rate and precision of estimated biomass.

with $(V/R^2) = 1/4$. In practice, annual adjustments of TACs are normally less than 30% due to autocorrelated estimation errors not included in the present model and due to assumptions of average levels for incoming recruitment which corresponds more closely to a constant catch level strategy.

Discussion

The influence of environmental fluctuations on the dynamics of exploited fish stocks has been studied previously by the application of random noise to general production models. Beddington and May (1977) considered the implications of replacing the growth rate parameter of Schaefer's (1954) quadratic production model with a constant plus a stationary white noise signal. Based on analysis of their simplified model, it was concluded that, for a population harvested in a randomly varying environment, the relative variability in the population magnitude and yield increases with harvesting effort and that these effects are relatively more pronounced for a harvesting strategy seeking constant yield. Similar conclusions were reached by the present author (Doubleday 1976) for a discrete time version of the Schaeffer model and in the review by May et al. (1978). However, depending on the stability of the unexploited population equilibrium and on how the stochastic element is introduced, the opposite can theoretically occur (May et al. 1978; Shepherd and Horwood 1979). Other studies (e.g. Ricker 1958; Mendelssohn 1982) have examined similar problems for Pacific salmon where the focus is on relations between parent stock and subsequent recruitment.

The present study confirms these general observations for a different model that more closely corresponds to what is known of the population dynamics of exploited herring stocks, explores the impact of imperfect estimation of abundance, and provides quantification of the general conclusions.

The applicability of the simple model (2) allows conclusion (2) of the Aberdeen Symposium to be refined. For the model, the ratio of production to biomass is

$$P/B = a - 1 + a(R_t - C_t)/B_t$$

in which only the recruitment term shows higher productivity at lower stock sizes. A decline in the mean age of mature herring has little impact on the productivity per ton of biomass via increased growth rates, increasing net production by only a few percent. Thus, when a herring stock is exploited, the spawning biomass has very little resilience. This is in stark contrast with cod and many other groundfish species where growth declines more slowly with age, and maturity occurs at a lower fraction of L_∞ (e.g. 31% for southern Gulf of St. Lawrence cod, Ware (1980)) leading to larger increases in productivity per ton when the mean age is reduced and where reduced biomass is frequently associated with increased growth rates at age. For herring, new recruitment is by far the dominant, and also the most variable, factor in spawning stock production.

The implication of this distribution of production is that herring stocks are less able to sustain heavy exploitation than are most groundfish stocks. Also, the response is delayed and uncertain because of the dependence on recruitment. This slow response can be exacerbated, as in the case of North Sea herring, by extensive fishing of juveniles.

Thus, the relatively low P/B ratio for herring only partly explains its vulnerability to fishing. More precisely, positive net production for the spawning stock comes only from recruitment and not from the usual excess of growth over natural mortality for a fished stock, and the lack of a significant increase in

productivity per ton of mature biomass through changes in the mean age or growth rates at age implies that for moderate to high exploitation rates, poor recruitment for 1 or 2 consecutive yr leads to a rapid decline of the spawning stock biomass. This form of vulnerability is exacerbated by schooling behaviour that allows high catch rates to be maintained at low stock sizes. For many groundfish species, especially cod, the impact of 1 or 2 yr of poor recruitment is compensated for by increased growth of the remaining spawning stock.

The usual reference point for setting herring catch levels in Atlantic Canada and Europe is the estimated catch at $F_{0.1}$.[2] In recent scientific advice, catch levels below $F_{0.1}$ have been advised in cases of low stock size. Examples are a target $F = 0.1$ for North Sea herring (ICES Advisory Committee on Fishery Management (ACFM), May 1, 1983) and Southern Gulf of St. Lawrence where closure was recommended from a biological point of view by the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) in May 1983.

For the model analysed here, exploitation rates of 0.3 and higher result in substantial reduction of spawning stock size from unexploited levels and lead to the occurrence of spawning stock sizes of less than (the biomass at the time of maturation of) one average recruiting year-class more than once every 10 yr. Such low levels may lead to reduced subsequent recruitment and are very likely to result in debate on the need to temporarily close or drastically cut back the fishery. An exploitation rate of 0.3 is not much different from a fishing mortality rate of 0.3, which is $F_{0.1}$ for several herring fisheries. Thus, the policy of fishing at $F_{0.1}$ is not a conservative policy for herring and could lead to stock collapse. It is ironic that $F_{0.1}$ for many cod fisheries is about 0.2, which is much lower than the same reference point for herring fisheries that are less robust. Adoption of an exploitation rate of about 0.2 or lower results in considerably greater stability of spawning stock size and very rare occurrence of levels below one average recruiting year-class. Thus, it appears that a target fishing mortality rate of 0.2 is more appropriate for management of herring fisheries on a sustainable basis than is $F_{0.1}$. For the model studied, policies aimed at catching more than 70% of the theoretical maximum yield result in unstable spawning biomasses with low average levels. This result allows conclusion (3) of the Aberdeen Symposium to be refined, namely that exploitation rates of 0.3 or higher lead to frequent occurrence of low spawning biomasses allowing any latent stock and recruitment relation to become effective.

The tendency of catch rates to remain high when abundance is low and the need for fishermen to maintain incomes complicated the management of herring fisheries by creating pressures to maintain constant catch levels despite declining stocks. As noted in earlier studies, such a practice results in less stable stock biomasses than a constant exploitation rate strategy. Analysis of the present model as illustrated in Fig. 13 shows that to obtain the same level of stability of the spawning stock (in terms of CV) as would result from a given constant exploitation rate, a constant catch strategy would have a smaller catch than the average catch under the constant exploitation rate alternative. The difference is greatest near the proposed target exploitation rate of 0.2 and can represent more than 20% of the average yield for the constant exploitation rate strategy.

The importance of accurate abundance estimates depends on the exploitation rate. For low exploitation rates, near 0.2 or less, the main impact of imprecise abundance estimates is increased year to year variation in catch quotas. This increased variability is due to changes in estimates that do not correspond to changes in stocks and would undermine scientific credibility but would not have any significant impact on the dynamics of the spawning stock involved. In practice, advice on catch levels can be expected to vary less from year to year than would be expected from the nominal level of precision of abundance estimates, due to the accumulation of information over several years (positively correlated errors of estimation) and assumptions that future recruitment will be at some average level. When exploitation rates are high, however, imprecise information leads to widely varying exploitation rates and destabilization of spawning stock biomass (Fig. 13). Thus, from the point of view of stock stability, more accurate information on abundance is needed when target exploitation rates are higher, particularly at or above the $F_{0.1}$ level of 0.3.

The impact of varying compositions of catches in mixed fisheries has been dealt with only qualitatively in the present analysis. So little reliable information is available on variable mixing rates in practice that any model of the process must be arbitrary. Nevertheless, the example of Southern Gulf of St. Lawrence herring shows that assumptions of constant mixing rates can be very far from the truth and it is obvious that wide fluctuations in mixing rates, of the order of 20–80%, would lead to corresponding fluctuations of fishing mortality on component stocks of a mixed fishery. If the average fishing mortality in the mixed fishery is already high, such variable mixing rates can lead to very high mortality for some components of the mixed fishery. Thus, mixed stock fisheries complicate the problem of managing a fishery to achieve a target fishing mortality rate as well as making the monitoring of catches and fishing mortality on a stock basis more difficult and less certain.

Conclusions

(1) Because of the lack of resilience of adult herring stocks under exploitation, recruitment to the fishery is more important relative to growth of recruited fish than in many groundfish fisheries.

(2) Attempting to harvest catches near the theoretical maximum yield per recruit leads to a very unstable spawning stock size as well as inviting any stock–recruit relation to become effective.

(3) An average exploitation rate of 0.2 of the spawning stock and biomass estimates with a CV of 0.4 or better would allow about 70% of the theoretical maximum yield to be taken without dramatically reducing and destabilizing the spawning stocks.

(4) Herring fisheries become more manageable, from a biological point of view, as mixed fisheries represent less of the total catch. The potential for high exploitation rates on some component populations increases in proportion to the exploitation rate of the mixed fishery and the variability of mixing proportions.

(5) If the exploitation rate exceeds 0.3, decline of spawning stock size to less than one average recruiting year-class must be expected more than once every 10 yr.

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[2] $F_{0.1}$ is the rate of fishing mortality at which the slope of the yield-per-recruit curve is 1/10 the value at zero fishing mortality; for Canadian Atlantic herring fisheries it is near 0.3.

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Appendix

Given the assumptions that (1) a is a constant greater than 0 and less than 1, (2) $R(t)$, the recruiting biomass in year t, is an independent, identically distributed series of random variables with mean R and variance Σ, and (3) $C(t)$ the annual catch in weight is constant, a constant fraction of the current total biomass $B(t) + R(t)$, or a constant fraction of an estimator of total biomass which is unbiased and has independent, identically distributed estimation errors in different years which are also independent of $R(t)$ and $B(t)$, then $B(t)$ as defined by the relation

$$B(t+1) = a(B(t) + R(t) - C(t))$$

is a stationary first-order linear autoregressive stochastic process. Over a period of years, the probability distribution of biomass and catch converges to a time in-variant (stationary, ergodic) distribution (Cox and Miller (1965)). Formulas for equilibrium means and variances are as follows:

Case 1: $C(t)$ is constant:

Mean catch: $E[C(t)] = C$

Mean biomass: $E[B(t)] = \dfrac{a(R-C)}{1-a}$

Variance of biomass: $\mathrm{VAR}[B(t)] = \dfrac{a^2\Sigma}{1-a^2}$

Coefficient of variation of biomass:

$$\mathrm{CV}[B(t)] = \left(\frac{\Sigma(1-a)}{(1+a)}\right)^{1/2} \times \frac{1}{R-C}.$$

Case 2: $C(t) = \gamma(B(t) = R(t))$ where γ is a constant, $0 \leq \gamma < 1$:

Mean catch: $E[C(t)] = \dfrac{\gamma R}{1-a(1-\gamma)}$

Mean biomass: $E[B(t)] = \dfrac{a(1-\gamma)R}{1-a(1-\gamma)}$

Variance of biomass: $\mathrm{VAR}[B(t)] = \dfrac{a^2(1-\gamma)^2\Sigma}{1-a^2(1-\gamma)^2}$

Coefficient of variation of biomass:

$$\mathrm{CV}[B(t)] = \left(\frac{1-a(1-\gamma)}{1+a(1-\gamma)} \times \frac{\Sigma}{R^2}\right)^{1/2}$$

Case 3: $C(t) = Q(t)$ where γ is a constant, $0 \leq \gamma < 1$ and $Q(t)$ is an estimate of $B(t) + R(t)$ such that $E[Q(t)] = B(t) + R(t)$, $\mathrm{VAR}[Q(t)] = V$, a constant, and $Q(t) - B(t) - R(t)$ is statistically independent of $Q(t')$ for $t \neq t'$ and of $B(t'')$ and $R(t'')$ for all t'':

Mean catch: $E[C(t)] = \dfrac{\gamma R}{1-a(1-\gamma)}$

Mean biomass: $E[B(t)] = \dfrac{a(1-\gamma)R}{1-a(1-\gamma)}$

Variance of biomass: $E[B(t)] = \dfrac{a^2(1-\gamma)^2\Sigma + a^2\gamma^2 V}{1-a^2(1-\gamma)^2}$

Coefficient of variation of biomass:

$$\mathrm{CV}[B(t)] = \left(\frac{1-a(1-\gamma)}{1+a(1-\gamma)} \times \frac{(1-\gamma)^2\Sigma + \gamma^2 V}{(1-\gamma)^2 R^2}\right)^{1/2}$$

Variance of catch:

$$\mathrm{VAR}[C(t)] = \gamma^2 \frac{(\Sigma + V(1-a^2((1-\gamma)^2 - \gamma^2)))}{1-a^2(1-\gamma)^2}.$$

The Need for Formalization of Decision Algorithms and Risk Levels in Fishery Research and Management[1]

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Application of the principles of error analysis and use of decision algorithms might significantly improve fishery management and provide a formalized method of priority allocation and justification of research effort. Verification of this thesis would also provide specific measures of the value of improved data on management success, which at present apparently do not exist. In several fisheries, research and management has reached the stage where codification of the decision making procedures is possible. The development of such decision algorithms coupled with statements of acceptable harvest risks could permit measurable efficiencies in management through a clear indication of the levels of precision and accuracy required for each step in the procedure. Firmly established techniques are available. Analysis of error as employed in geodetic surveying and in physics can serve as a basis for applying the principles to fishery management. The advantages to research and management agencies of the acceptable risk approach is in formally defining priorities for investigation through specification of precision, accuracy, and timeliness of each component of information. The necessary sampling and survey effort can be quantified in terms of acceptable error and provides budget justification. Perhaps the most compelling reason to evaluate these concepts is that their application would require the participation in risk evaluation of fishermen and industry with the management agency. This would provide a basis for mutual understanding of resource decision making and the rationale of prediction for the users. Attempts at applying the procedures to the British Columbia roe herring fishery are described and possible solutions to existing problems recommended.

L'application des principes de l'analyse d'erreur et l'utilisation des algorithmes de décision permettaient d'améliorer de façon appréciable la gestion des pêches et fournirait une méthode formelle pour l'établissement des priorités et la justification des efforts de recherche. La vérification de cette thèse permettrait aussi d'obtenir des mesures précises de la valeur des données améliorées sur le succès de la gestion, qui semblent actuellement faire défaut. La recherche et la gestion de plusieurs pêches ont maintenant atteint un stade où il est possible de codifier les procédures décisionnelles. L'élaboration de tels algorithms décisionnels utilisés de pair avec des énoncés de risques d'exploitation acceptables devrait permettre de mesurer l'efficacité de la gestion grâce à la connaissance des niveaux de précision et d'exactitude nécessaires à chaque étape de la procédure. Nous disposons de techniques très bien établies. L'analyse d'erreur utilisée dans les domaines des levés géodésiques et de la physique peut servir de base à l'application de ces principes à la gestion des pêches. Les avantages que représente l'approche par risques acceptables pour la recherche et la gestion résident dans la définition formelle des priorités de recherche par la spécification de la précision, de l'exactitude et du moment d'obtention de chaque composante d'information. Les échantillonnages et les relevés peuvent être quantifiés en fonction de l'erreur acceptable et permettre la justification des budjets. La plus importante raison d'évaluer ces concepts tient peut-être dans leur application qui nécessiterait, lors de l'évaluation des risques, la collaboration des pêcheurs et de l'industrie avec l'organisme de gestion. Cela favoriserait la compréhension du processus décisionnel appliqué aux ressources et permettrait aux usagers de connaître les raisons des précisions. On décrit un essai d'application de ces procédures à la pêche au hareng plein en Colombie-Britannique et propose des solutions à certains problèmes.

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In the 75 yr since the Nanaimo Biological Station was founded, fishery science has made some great strides but the progress has been very uneven. This uneveness is not only by geographical region and by species, but within areas of research and management itself. With some types of problems, our skills are considerable and possible precision high (e.g. growth studies). In others, our ability is often dignified by the word "guesstimate" (e.g. natural mortality).

Over time, many models and procedures have been developed for the management of fishery resources. In all cases where details are available, the output of formal predictions is modified by judgement. The methodology of judgement is not formalized so that it is unlikely that two or more individuals

[1]This paper was presented at the International Symposium on the Biological Characteristics of Herring and Their Implication for Management, convened at Nanaimo, B.C., June 20–22, 1983, commemorating the 75th anniversary of the Pacific Biological Station.

would arrive at the same management recommendations or even have the ability to trace the other's logic.

The reasons for applying adjustments are that data of varying quality, that is, of differing precision and accuracy, have to be combined.

It appears that if we can collect data to great precision, regardless of cost, we usually do so, and then combine it with information differing in quality by orders of magnitude or even with outright guesses. We have all read papers where the optimum age of first capture is calculated to several decimal places, while natural mortality is guessed to one decimal place.

In final analysis, these adjustments are a consequence of a lack of guidance on degree of accuracy and precision required, which in turn are dependent upon the biological, economic, and social risks that we are willing to assume, which in large part may be stated statistically.

In general, we are all aware of sample size calculations and the concept of type I and II errors wherein we state in advance the likelihood that an hypothesis is wrong when we estimate it to be correct and vice versa. But even in fundamental fishery research, the methods are only infrequently applied with rigor.

The thesis of this paper is that the time is ripe to codify management procedures into decision algorithms (algorithm: "a step-by-step procedure for solving a problem or accomplishing some end" (Webster's Ninth New Collegiate Dictionary)), to define appropriate risks, and apply concepts of propagation of error to define precision, accuracy, and timeliness in our data acquisition. This process would clearly identify specific data as well as lacunae that could define investigative priorities and substantiate budget requests with more firmness than any of the techniques, formal or otherwise, employed to date.

Further, application of such procedures would provide measures of the value and costs of improved data on the management process. Such information does not exist in a quantifiable fashion at the present time. With few and qualified exceptions (e.g. Walker et al. 1983), simulation models thus far have only treated the problem in a relative and theoretical way. This, in turn, explains why there are no formal objective criteria for measuring the success and/or failure of a fishery. This appears to be so whether we are describing biological, economic, or institutional performance. There is an urgent need for objective performance criteria; otherwise, objective measurement of the management process is not possible.

In discussing planning, priorities, and budget, it is important to identify the categories of management information, which may meet needs for (1) safe-fail monitoring, (2) immediate management, (3) remedial improvement and enhancement, and (4) research and development information to support (1) to (3). The nature of these elements is treated in the Advisory Committee on Marine Research and Resources (ACMRR) Report of 1979 (Wilimovsky 1980). This paper is devoted to the first two items though the principles are applicable to all four categories.

In several fisheries, research and management has reached the stage where codification of the decision making procedures is possible. The development of such decision algorithms coupled with statements of acceptable harvest risks could permit measurable efficiencies in management through a clear indication of the levels of precision and accuracy required for each step in the procedures and their probable costs.

Two approaches, theoretically complementary, are possible in these analyses: those of prediction and hindsight. In fact, they differ in practice. *Predictive* — given the objective and acceptable risks, to calculate the precision required at each step of analysis, thus defining the sampling requirements and their costs. *Hindsight* — given the precision of each analytical step, to calculate the limits of confidence about the estimates of final values.

Unfortunately, the second alternative does not usually involve the discipline or rigor required in the predictive case. Ordinarily, less attention is given to the estimate of confidence limits in retrospective analysis, whereas in the predictive mode, the necessary consultation in developing risk levels makes that procedure much more robust.

In either mode of analysis, required are (i) a firm and concise statement of objectives, (ii) development of acceptable risk levels, (iii) codification of field practice and analytical procedures into decision algorithms, (iv) application of error analysis to determine precision requirements, and (v) calculation of sample size, sequence of operations, and costs for field surveys.

These few steps warrant discussion. The primary caveat is that the principles employed in this type of analysis are appropriate only to fisheries with mature data bases. i.e. where time series and previous analysis have given an indication of the nature of the processes involved.

The *objective statement* usually requires policy input and ordinarily cannot be prepared in the confines of a single discipline, since it requires economic and institutional input. It is important to clearly identify the problem boundaries. If too broad in scope the objective becomes diffuse and measurement of achievement much more complex. If the task is large it is wise to modularize the problem. It is important to recognize the consequences of short-term versus long-term planning in preparing such a concise objective statement. Short-term efforts usually involve suboptimal goals whereas the long-term objective is optimality of some kind.

Development of total allowable catches (TACs) and management plans have already gone a long way in considering such questions as well as those of the next element.

Establishment of *acceptable risk levels* ordinarily requires analysis in a top-down or end-use fashion. Significantly, input is required from all participants: fishermen, processors, government. While such a consultation can be tedious, it provides a firm basis for understanding and conflict resolution.

Decision algorithms are familiar to most, particularly those working with models, for the very process of computer programming requires their employment. The additional requirement proposed here is the codification of field judgements so as to spell out the estimations and "gut feeling" procedures so universal in fisheries management today.

The application of *error analysis* requires conversion of the algorithm to a mathematical functional form with the purpose of determining the precision required at each step of the management process. (Or in the retrospective case, the confidence level of the final estimates.) The technique of error analysis is firmly established and widely employed in geodesy, first-order surveying, and throughout physics (especially thermodynamics). Use of the computer makes the calculation of the many partial derivatives necessary for analysis relatively easy. Procedures are analogous to those familiar in beginning physics: to what resolution must you measure each side of a rectangle to calculate the area with a confidence range of x percent. While fishery management functions are far more complicated, the same principles apply.

Beers (1953) provided a concise introduction to the theory of error, and any recent edition of Scarborough's *Numerical*

Mathematical Analysis (e.g. Scarborough 1962) treats the subject in a rigorous manner. Numerous other works treat the subject.

Given the precision required, the *sampling procedure, sample size, and cost* may be determined. Silvert (1978) and more recently Schweigert and Sibert (1983) have approached the costing and performance issues in sampling herring for given accuracies and precisions.

It is important to recognize that it is possible one cannot achieve the required precision. The required remedial action to obtain the necessary precision establishes direction in the sense of priorities and importance either by indicating improvement of techniques within a given time frame and/or cost or by recognizing the fact of the limited precision in the risk evaluation calculation.

Determining the value of added information to the management process is more difficult. Simulation approaches to this question have been limited to production increments. Silvert (1978), Huang et al. (1976), and others have attempted to quantify the management value of added information but these studies are very theoretical and much additional work is needed to bring their application to a practical stage.

In spite of first impressions, none of the aforementioned involves a great deal of additional effort and all can be justified as good science having immediate practical importance in research and management areas. The necessary discipline of thinking through what are appropriate levels of risk will likely turn out to be an iterative approach involving all the components of the fishery, particularly industry and fishermen. The overall gain will be apparent to all participants by providing the basis for management actions in a clearly documented fashion. The acceptable limits of error developed jointly by the users should permit more rational prediction of performance of a given fishery and profitability as well as understanding of the management process. These decision making procedures, or algorithms, can allocate specific responsibility, pinpoint the weaknesses in the system and knowledge, and lead to a clear understanding of the mechanism. This, in turn, can provide for allocation of priorities as well as their firm justification in terms of funding as the costs of data acquisition can be calculated.

Analysis of propagation of error is not a panacea for solution of fishery problems but it certainly can assist in establishing a framework for formal judgement where priorities and precision need to be applied.

In the past few years while developing this subject, it became apparent to me that there are many interpretations of the concept of planning as well as concerns over the consequences of this approach to fishery management, particularly in the area of priority allocation. Many are based on misunderstandings, but as a thrust, these collective concerns prove to be a major deterrent to even trying to apply these approaches. The reluctance to change is great. Apparently, some individuals feel that quantification of the rule making process and elimination of the human adjustment or fudgefactor deprives the manager of options and flexibility in operation and is a reflection on his or her judgement. Others take the view that formalization and algorithms fix one in "concrete." Still others believe that direct involvement of fishermen and the industry in decision making "can never work" in fishery resource management. My own interpretation is that this analytical process, through the fixing of responsibility for action, helps to establish and define the areas of strength or weakness and point out where additional research and information are needed. Often of real concern, under present conditions of fiscal restraint, is the view that if one makes an improvement and requires fewer personnel and/or funds to do the job, budget and staff will be reduced and the project is thrust back to where it began. These kinds of problems can be eliminated only if there is agreement and understanding on the purposes of the plan and the algorithms involved.

To bring about this shift in management philosophy requires a clear understanding of the components of information and limits of accuracy and precision in the various kinds of research and management information we are collecting. The ACMRR (FAO) (1974) treated the desirable characteristics of information in detail. The five components are listed in the following table:

Identification and definition of information requirements

Scope and relevance Timeliness Accuracy and precision Clarity and ease of comprehension Acceptability and credibility	+ stopping rules

The result of failure to recognize these characteristics is documented in a series of case studies reported by Hilborn (1979) and those cited by him. The process of bringing about change and change agents has received considerable attention in the professional management field and these techniques are just beginning to surface among progressive fishery management agencies. However, it is unlikely that major change will come about in management philosophy unless a clear demonstration of the advantages of the approach proposed here can be demonstrated.

A brief review of an attempt to apply this technique to a north temperate fishery may be in order. The British Columbia roe herring fishery approaches the necessary mature data base in biology but is much limited in publicly available economic information. Most institutional data are anecdotal. The current annual cost of management of the British Columbia herring resource is $3.26 million and involves 53 person-years of effort (Fig. 1). About 68% of the total cost is devoted to data acquisition. Substantial additional effort in data acquisition is also included in the 21% of costs devoted to management. In addition to the foregoing, at current harvest levels of 40 kilotons, industry costs not including capital costs have been estimated at $83 million ± $2 million. These same sources estimate that industry gross income is $85 million ± $2 million. Thus, the fishery may be close to a breakeven point in terms of dollars. This is not to imply that fishermen are satisfied with their current earnings. Of course, there are other criteria for judgement such as GNP, employment, regional development, native peoples, environment, etc. Nevertheless, the large proportion of management costs devoted to data acquisition suggests that there is considerable scope for improvement.

With the cooperation of fisheries personnel from many divisions, several fishermen, and a significant representation from industry, I found that applying the analysis was easier said than done, primarily because the problem had never been approached in this fashion. Significantly, many of the data were available in other forms.

As the nature of the herring roe fishery has been ably reviewed by several authors in this Synmposium issue, familiarity with current management practices is assumed.

My comments proceed from the user end in reporting the

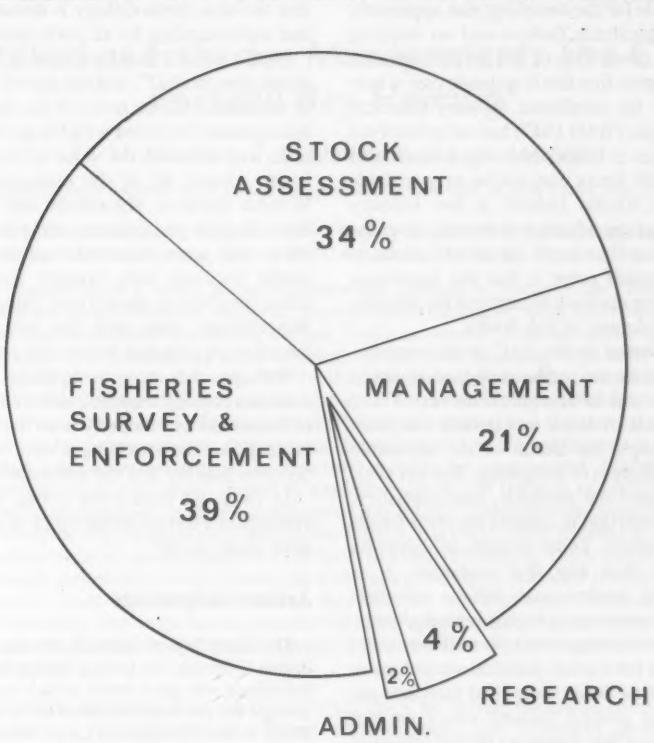

FIG. 1. Management costs for the British Columbia herring resource (data derived from the Department of Fisheries and Oceans).

views of the processor and fishermen before commenting on the problems of the management agency.

The industry members interviewed appear to be satisfied with the TAC (total allowable catch or quota) approach, as it permits advanced planning and allocation of harvest and processing resources. Two core problems are the seasonal availability of fish, which is of concern to the fishermen, and the estimation of egg maturity, which is central to the success of the buyer and processor.

Because of the time lags in financial investments and payments by the fishermen, short of bankruptcy there apparently is no stopping rule for fishermen associated with availability of fish. As long as there is any chance of success, fishing will proceed. It is discouraging to report that many of the attitudes of fishermen reflect little faith in the management process, that there is little trust in current predictions, the view being that "the department of fisheries does little for me, it is only there to protect the fish." Nevertheless, on more serious consideration, many fishermen concede that their success might be improved if they had timely information on current fleet distribution. Modelling the fishing operation is complicated because many elements affect fishing success. The decision algorithms and measurement of the value of such information to improvement has very broad requirements, some of which at present are intractable. Hopefully, the current studies of the behavior of salmon fishermen by R. Hilborn and M. Ledbetter (pers. comm.) may provide a codification to the actual fishing process or better insights to the process that might be applied to herring.

Availability of fish to the processor at low or intermediate levels poses no serious problems, as the industry is capable of handling between 2400 and 2600 tons per day if landings are sporadic. On a continuous basis, freezer capacity limits daily input to 1200–1800 tons depending upon whom you contact. This is a good example of a data element clarification, as this range of uncertainty would have a sizeable effect on risk level evaluations. Beyond this rate of landings, the inspection branch of the Department of Fisheries and Oceans believes that quality of product is affected. Presumably, if this is a frequent occurrence, additional mechanisms for control of this frenzied harvest would be required.

More central to the processing issue is the estimation of egg maturity. There is no risk to industry (i.e. processor) if the error is made on the high side of the acceptable value but if the maturity estimate is less than the stated amount by only 2 percentage points, according to some industry representatives the margin of profit drops to zero. There seems to be no dispute over the methods of determining egg maturity, and representatives of all parties concerned participate in its determination.

The issue is the adequacy of the sample in relation to the stocks being harvested. The rationale for the sampling plan apparently is not documented in an algorithmic fashion and no stopping rules exist that relate to the down side of the present unstated confidence limit. It would appear that this is a classic case where sequential sampling might be employed to very practical benefit. This efficient technique (Wald 1947) has never received the application that it deserves in fishery investigations. It also must be mentioned that the 2% figure may not be an acceptable value to the industry as a whole. Indeed, a few industry representatives suggested that specifying a downside level for risk is proprietary information that could be advantageous to their competitors. The important point is that the processors interviewed believe developing decision algorithms for industry is possible, including establishment of risk levels.

Since the foregoing is all based on the TAC level, considerable time was spent in analyzing the methods of assessment of stocks and determining the levels of acceptable harvest. There are, in general, three methods of stock assessment that have been employed for determining the extent of the allowable fishery. All involve varying degrees of weighting. Stocker et al. (1983) have recently compared the methods, characteristics, and in particular have been forthright in identifying areas where empirical weightings are involved. These weights are based on "feelings" of errors rather than any real measures. It is interesting that even among professional fishery scientists opinions regarding extent of errors seem highly biased. Apparently, fishery scientists are very impressed by outliers in the data, again stressing the need for a set of decision algorithms in making error judgements. These basic biological forecasts are further tempered for varying general reasons which are not documented with the suggestion that managers should take only 50–60% of the potentially fishable stock.

By the time such economic and institutional restraints as the concern of sport fish and other lobbies are added we are now back to taking only 20% of the stock size, which was the field managers original "gut feeling." This observation has raised a serious query as to why we do research. Would not management of the fishery proceed at the same level of competence without it?

Without a set of decision algorithms and a clear statement of acceptable risks, there appears to be no quantitative way to evaluate the value of increased information on management performance. As previously noted, there is no difficulty in considering mathematical models as decision algorithms. What is required is the formalization of the estimation procedures which in themselves comprise years of valuable field experience and are virtually undocumented even in internal reports. The Department of Fisheries and Oceans is currently trying a novel approach. It is using members of peer groups to collect such information. For example, a field officer has been assigned to collect and attempt to quantify the methods used by field personnel in making judgements. Hopefully the results of this effort will be made available for evaluation.

It appears that it will be relatively easy to determine the costs of data acquisition of the various steps of management. Current computerization of Department of Fisheries and Oceans budget information will allow manipulation of such data so that the costs may be ferreted out if the needs for increased detail can be justified.

In spite of my initial frustrations in this study, it became apparent to me that there are several opportunities if sufficient authority and support are given to test that approach. Further, it has been my experience that when agreement on risk estimates and decision methodology is documented, a new level of trust and understanding by all participants is achieved.

At this point a usual question is "why not do all of this with a simulation model?", and the answer lies in the area of evaluation of its results. Since most of the inputs at all levels of herring management involved weightings of a "gut feeling" kind, there is no way to assess the value of improved data on an objective basis. Almost all of the management wisdom is empirical. Without decision algorithms and risk estimates that require input from all participants, one cannot realistically measure the effort and costs involved, and any such limited simulation model becomes only broadly representative. Consequently, initial progress in quantifying these values is likely to be slow. Nevertheless, costs and clear budget justification seem worth the effort to continue to test this method.

Perhaps the most compelling reason to evaluate these concepts is that their application would require the participation of fishermen and industry with the management agency in risk evaluation, thus providing a basis for understanding of resource decision making and the rationale for management.

In 75 yr, we have come a long way. Is it not appropriate to evaluate in a formal sense which of our efforts have been proven to be most useful?

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The feasibility of applying the aforementioned techniques to the British Columbia roe herring fishery has been greatly aided by many individuals who gave freely of their time and background experience through the provision of data and by informative discussions. Allen Wood, Robert Humphries, Lloyd Webb, and Daniel Nomura deserve special thanks. None of them are to be held responsible for my interpretation of the information.

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Fortuity Disguised as Fisheries Management: The Case History of Fortune Bay Herring[1]

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Winters, G. H., E. L. Dalley, and J. A. Moores. 1985. Fortuity disguised as fisheries management: the case history of Fortune Bay herring. Can. J. Fish. Aquat. Sci. 42(Suppl. 1): 263–274.

The population dynamics of a stock of spring-spawning herring in Fortune Bay, Newfoundland, are described in relation to exploitation patterns, management strategies, and environmental variability. Biomass levels increased substantially during the late 1960's as a result of the recruitment of several strong year-classes that were pulse-fished by a purse-seine fishery. The resulting high fishing mortality rates caused a rapid stock decline in the early 1970's that was associated with an increase in the partial recruitment rate of the younger age-groups as well as an increase in the catchability coefficient of the purse-seine fleet. The combination of these classical changes resulted in a substantial overestimation of stock abundance and recruitment levels that was not corrected until an alternative series of catch rates and partial recruitment estimators were used to fine-tune population assessment. Environmental factors, rather than spawning stock size, were shown to explain a significant fraction of recruitment variability. Alternative fishing strategies such as the $F_{0.1}$ and surplus production concepts were simulated and shown to be less efficient in extracting biomass yield than pulse-fishing. It is concluded, therefore, that management regimes whose objectives are promulgated on the basis of stock rebuilding, stock stability, and enhanced recruitment through protection of the spawning stock are unlikely to succeed (except fortuitously) for herring populations such as those in Fortune Bay due to the dominant controlling influence of environmental variability. For such herring stocks the most appropriate long-term management strategy that could be supported on biological grounds would be a minimum size limit established at or above the length of 50% maturity.

Les auteurs décrivent la dynamique de population d'un stock de hareng frayant au printemps dans la baie Fortune (Terre-Neuve), relativement au schème d'exploitation, aux stratégies gestionnelles et à la variabilité environnementale. Vers la fin des années 1960, la biomasse a augmenté considérablement à la suite du recrutement de plusieurs classes d'âge puissantes, pêchées intensément à l'aide de sennes coulissantes. Les taux élevés de mortalité par pêche qui en résultèrent ont entraîné une baisse rapide du stock au début des années 1970, baisse associée à une augmentation du taux partiel de recrutement des plus jeunes groupes d'âge ainsi qu'à un accroissement du coefficient de capturabilité de la flottille de senneurs. La combinaison de ces variations classiques a mené à une surestimation importante de l'abondance du stock et des niveaux de recrutement, surestimation qui ne fut corrigée que lorsqu'une autre série de taux de capture et de facteurs d'estimation du recrutement partiel a été utilisée pour mettre au point l'évaluation de la population. Des facteurs environnementaux, et non la taille du stock reproducteur, justifient une importante fraction de la variabilité du recrutement. D'autres stratégies simulées de pêche, dont les concepts de $F_{0.1}$ et de la production supplémentaire, se sont révélées moins efficaces que la pêche pulsatoire pour l'extraction du rendement de la biomasse. Les auteurs en déduisent donc que des régimes gestionnels dont les objectifs se fondent sur la reconstitution du stock sur sa stabilité et sur un recrutement accru par la protection du stock reproducteur ont peu de chance de réussir (sauf par hasard) pour des populations de hareng comme celles de la baie Fortune à cause de l'influence dominante et déterminante de la variabilité environnementale. Pour ces stocks de hareng, une limite de taille minimale (égale ou supérieure à la longueur quand 50% des individus sont matures) représenterait la stratégie gestionnelle à long terme la plus appropriée qui pourrait être appuyée par des données biologiques.

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Traditionally, until the mid-1950s, Fortune Bay on the south coast of Newfoundland (Fig. 1) was one of the main centres of the Newfoundland herring fishery (Templeman 1966). During the immediate post World War II period (1945–50) average annual landings of herring from Fortune Bay were 16 000 metric tons (t) and were sold mainly in the form of salted herring, which was then in great demand by the United Nations Relief Agency (UNRA) for the rehabilitation of war-torn Europe. During the 1950's, however, annual landings declined to less than 700 t (Templeman 1966) mainly as a result of reduced demand for herring as food but also due to the disappearance of herring from traditional areas (Parsons and Hodder 1973) possibly in association with a

[1]This paper was presented at the International Symposium on the Biological Characteristics of Herring and Their Implication for Management, convened at Nanaimo, B.C., June 20–22, 1983, commemorating the 75th anniversary of the Pacific Biological Station.

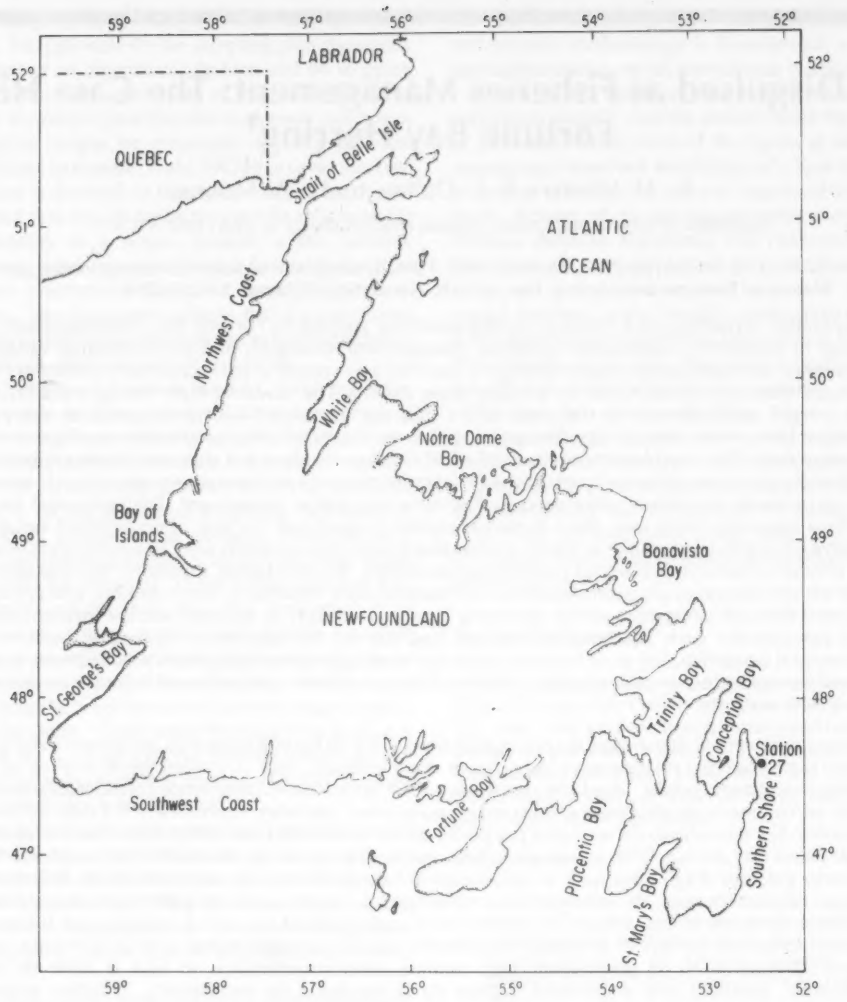

FIG. 1. Area map showing locations mentioned in the text.

fungus disease that destroyed a substantial portion of the southern Gulf of St. Lawrence herring stock during 1953–57 (Sinderman 1958). The resumption of the Fortune Bay herring fishery in the late 1960's was concomitant with the rise in demand for fish meal and the associated expansion of the Atlantic purse-seine fleet into Newfoundland waters (Winters and Hodder 1975). During this period the Fortune Bay herring fishery was based on aggregations of immature and prespawning herring (mainly spring spawners) that appear in inshore areas during the January–May period (Parsons and Hodder 1973). Tagging studies (Moores and Winters 1979) and a comparison of various biological characteristics (Parsons 1973; Parsons and Hodder 1971) have shown that Fortune Bay spring spawners constitute a discrete herring stock.

This paper describes the population dynamics of Fortune Bay herring since the mid-1960's and attempts to evaluate the efficacy of recent management strategies in relation to environmental and density-dependent factors.

Materials and Methods

Random age and length frequency samples of herring caught in Fortune Bay are available since 1966. Age composition data were derived from otoliths, and in accordance with the recommended conventions (Hunt et al. 1973) age-groups have been used instead of ages. Thus, a fish is placed in age-group 0 in the year of its birth and enters the next age-group on January 1 of the succeeding year. All age composition data were initially compiled into monthly age-specific catches, which were then combined to represent the age composition of annual fishery removals. Age-specific maturation rates were derived from commercial sampling data broken down by length and age into mature and immature specimens. Maturity stages were assigned according to the eight-point scale recommended by ICES (Anonymous 1962).

Annual population fecundity (E) was calculated according to the following algorithm:

$$E = \Sigma M_t \cdot R_t \cdot N_t/2$$

where M_t = age-specific maturation rate, R_t = age-specific fecundity, and N_t = midyear population size at age.

Age-specific fecundities were calculated using average length-at-age from commercial sampling data (both sexes combined) and a fecundity–length relationship described by Hodder (1972) for Fortune Bay herring.

The population matrix of Fortune Bay herring for the period 1966–80 was reconstructed using a method of sequential population analysis developed by Pope (1972) and commonly referred to as cohort analysis.

Temperature and salinity data used are the mean monthly values for 0–20 m at station 27 (47°32′50″N, 52°35′10″W) near St. John's, Newfoundland (Fig. 1). This station provides the longest and most comprehensive data series available on changes in the marine climate in the Newfoundland area (Moores and Winters 1982). The surface layer was chosen because its physical characteristics (e.g. temperature and salinity) would be consistent with those under which egg development and early larval development of herring occurs, and, being above the thermocline, it would not be affected by annual or seasonal variations in the depth of that parameter.

Results

Trends in Fishery Parameters

Table 1 provides a breakdown of annual catches by gear for the period 1966–80. The rapid increase in total catches during the late 1960's was due primarily to the expansion of the purse-seine fleet into Fortune Bay from southwestern Newfoundland (Winters and Hodder 1975). The rapid decline in catches since 1971 is also most evident in purse-seine landings even though total allowable catch (TAC) levels were not restrictive. Since 1975, bar seines have been the major component in the fishery.

Age composition data of catches of herring in Fortune Bay (Fig. 2; Table 2) illustrate a characteristic feature of herring fisheries generally, i.e. catches being supported by a single dominant year-class, which is replaced in intermittent fashion by a subsequent dominant year-class. The purse-seine fleet entered the fishery in 1967 when a strong year-class (1963) was recruiting to the stock. This year-class dominated herring landings until 1969 when the 1966 year-class made a substantial contribution to annual removals. This was subsequently replaced by the strong 1968 year-class in 1970, and that year-class continued to dominate the fishery until 1976 when the 1974 year-class became dominant. Year-classes since 1974 have been weak and contributed less than 3% to the 1980 catch in terms of numbers landed.

Catch rate data are available from interview reports and landing records of the purse-seine fleet for the period 1967–73 and for the inshore gillnet fishery from landing records for the period 1978–80. The operating day, defined as the time between departure from and return to the landing port (but excluding known down-time due to inclement weather, etc.) was chosen as a measure of purse-seine effort, since it includes both searching time and fishing time. The purse-seine index (Table 3) indicates a seasonal decline in abundance from January–February to April; this is consistent with a real decline in abundance due to fishery removals and also a general dispersal of overwintering concentrations prior to spawning in late May. The apparent seasonal heterogeneity in catch rates was examined through use of a multiplicative model (Gavaris 1980). The results of this model indicated a highly significant seasonality factor (Table 4), which was then taken into account through a standardization procedure (Gavaris 1980). The standardized catch rates (Table 3) were high when the purse-seine fleet entered the fishery in 1967 but subsequently declined until 1970 when the strong 1968 year-class was recruited. Catch rates then declined dramatically to 1973.

TABLE 1. Component breakdown of Fortune Bay herring catches, 1966–80.

	Catch (t) by gear					
Year	Purse seine	Gill net	Bar seine	Other	Total	TAC
1966	—	193	—	—	193	—
1967	4 551	210	881	—	5 642	—
1968	11 686	122	2923	—	14 731	—
1969	4 837	440	1590	—	6 867	—
1970	7 920	425	1044	—	9 389	—
1971	14 579	226	200	—	15 005	—
1972	9 316	533	721	—	10 571	2500
1973	2 053	83	1117	1	3 254	4500
1974	1 928	72	268	—	2 268	4850
1975	809	19	81	—	909	3500
1976	109	43	310	—	462	3300
1977	188	22	364	5	579	1000
1978	105	42	853	—	1 000	1000
1979	286	76	829	1	1 192	1000
1980	897	84	265	—	446	200

Gillnet catch rate data (metric tons (t) per landing) are available only for 1978–80 (Table 5). They do, however, suggest that the decline in abundance observed in the purse-seine catch rate index was still continuing during the late 1970's and undoubtedly reflects the lack of significant recruitment to the stock during this period.

Reconstruction of Historical Population Matrix

Estimates of population size and fishing mortality rates for the period 1966–80 were obtained from cohort analyses (Pope 1972), the input parameters of which were determined as follows.

Partial recruitment rates (i.e. relative age-specific probability of capture) in the terminal year (1980) were calculated for each gear separately. The partial recruitment rate of gill nets was calculated from the gillnet mesh selectivity data provided by Olsen (1959) and applied to the 1980 commercial gillnet ($2\frac{5}{8}$-in. mesh) length frequencies at each age. Partial recruitment rates for the mobile gears (purse seine and bar seine) were calculated from the mean selectivity pattern exhibited by these gears for the years 1971–72 as estimated from trial runs of cohort analyses (Fig. 3A, 3B). The years 1971–72 were selected because of good sampling for those years and also because population estimates for these years are insensitive to the input parameters in 1980 (Fig. 5). The partial recruitment rate as derived from the weighted mean of the individual gears is shown in Table 6.

A natural mortality rate of $M = 0.20$ has been assumed. This is consistent with the growth and longevity characteristics of this stock in comparison with other herring stocks (Beverton 1963).

An estimate of the 1980 fully recruited fishing mortality (F_T) was derived from analysis of catch rates of gillnet fisheries in Fortune Bay (Table 5). Total instantaneous mortality rates (Z) were calculated for age-groups 4+ and 5+ by the method of

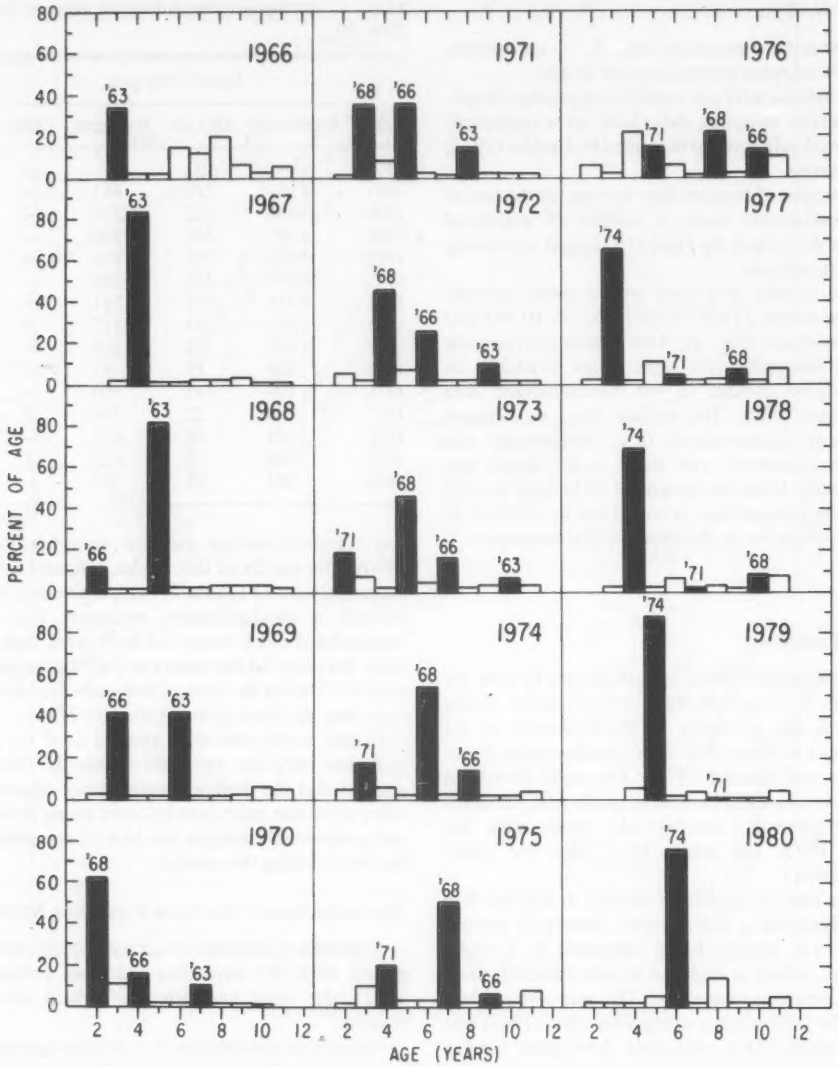

FIG. 2. Age compositions of commercial landings of spring-spawning herring in Fortune Bay, 1966–80. The dark blocks reference the strong year-classes.

Paloheimo (1961). The results (Table 7) indicated average total mortalities of 1.22–2.42 for 1978–79 and 0.52–0.53 for 1979–80. Given the much higher incidence of effort saampling in 1979 and 1980 and considering that the 1978 combined catch rate is heavily weighted by a single landing in June (Table 5), the 1979–80 estimate of Z was considered to be more reliable than the 1978–79 value. Consequently, cohort analysis was run such that the mean Z for 1979–80 (from cohort analyses) corresponded with the estimate of $Z = 0.53$ from the 1979–80 gillnet catch rate data. This was achieved with $F_T = 0.23$.

The population matrix for Fortune Bay herring as derived from the above parameters for the period 1966–80 is shown in Table 8, and the corresponding F-matrix is given in Table 9. The results indicate a good agreement between fishing mortality and fishing effort (Fig. 4A) and between biomass and purse-seine catch per unit of effort (CPUE) for the period of available data (1967–73), although similar results would have been obtained with a different level of terminal F (F_T).

Biomass levels of Fortune Bay herring were relatively high during the late 1960's and early 1970's due to the recruitment of three very strong year-classes in the 1960's of which the 1963 year-class was the strongest. With the exception of the 1974 year-class, which is only of moderate strength, all year-classes produced in the 1970's have been extremely poor. This pattern of recruitment combined with heavy fishing mortalities during the early 1970's (Table 9) resulted in a substantial stock attrition to the extent that in 1980 the estimated biomass (2+) was only 5% of the levels estimated for the late 1960's (Table 8). Biomass levels of Fortune Bay herring were also undoubtedly low during the early 1960's, as is indicated by the absence of a strong year-class previous to the 1963 year-class in the 1966 population matrix.

TABLE 2. Catch-at-age matrix of spring spawning herring from Fortune Bay, 1967–80.

	Catch-at-age ($\times 10^{-4}$)													
Age	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
2	<1	655	52	4238	17	154	222	39	<1	8	3	<1	<1	2
3	9	13	1198	800	2409	26	92	133	28	2	211	4	<1	2
4	2476	32	9	1043	631	1998	7	54	58	32	3	271	18	<1
5	5	4856	19	9	2436	294	567	12	11	23	33	6	383	7
6	5	22	1304	19	121	1094	46	457	9	13	17	24	2	111
7	42	12	19	731	20	36	175	12	149	1	3	4	17	1
8	45	61	26	24	939	11	8	112	2	34	4	14	1	18
9	51	77	69	2	14	540	5	1	14	4	19	5	2	<1
10	36	92	194	23	15	4	79	2	2	19	1	33	<1	1
11+	14	85	706	26	54	37	17	33	21	14	15	21	16	5

TABLE 3. Catch rate data of the purse-seine fleet operating in Fortune Bay during the period 1967–73. Numbers in parentheses refer to the effort (in operating days).

	Catch/operating day (t)				Standard catch rate	Estimated total fishing effort
Year	Jan.	Feb.	Mar.	Apr.	(Jan.–Apr.)	(operating days)
1967				41.5 (35)	65.1	87
1968		64.6 (67)	55.2 (70)	33.8 (51)	63.9	231
1969	62.3 (45)	34.8 (31)	47.6 (3)		51.3	134
1970	67.0 (57)	49.7 (25)	60.4 (40)	79.6 (6)	68.0	138
1971	48.3 (103)	59.4 (58)	50.4 (96)	32.6 (31)	56.0	268
1972	44.9 (75)	49.0 (11)	31.7 (128)	22.5 (68)	39.8	266
1973	22.1 (24)	22.1 (21)	18.7 (2)	38.3 (3)	26.5	123
Mean (weight)	51.0 (304)	52.0 (213)	45.3 (339)	32.5 (194)		

TABLE 4. Regression coefficients of purse-seine monthly catch rates as calculated by the multiplicative model of Gavaris (1980). F-value = 69.63 (3 df); $P < 0.01$.

Month	Regression coefficient
January	0.000
February	−0.076
March	−0.146
April	−0.471

An examination of the fishing mortality matrix (Table 9) indicates several patterns of change that are characteristic of purse-seine fisheries exploiting stocks of fish subject to periodic surges of recruitment. The temporal pattern of fishing mortality indicates that levels of F increased during the late 1960's and again during the early 1970's; these increases in F were both associated with good recruitment entering the fishery and are consistent with pulse-fishing characteristics. Also, the partial recruitment rates changed dramatically with the abrupt decline of the herring population in the early 1970's. For example, the partial recruitment at age-group 2 increased from an average of about 10% during the period 1967–69 to about 45% during the period 1972–74. Even though catches have remained at a low level since 1974, fishing mortality rates have continued to remain at about the 0.30 level.

Review of Management Strategies

The Fortune Bay herring stock was one of the first fish stocks in the Northwest Atlantic to be regulated by TAC, then in its early stages of development. A review of the assessment and management techniques as well as their efficacy is therefore in order, particularly since we now have fairly accurate estimates of population levels at least prior to 1978 due to the convergent nature of cohort analyses (Fig. 5).

The first TAC applied to removals of herring in Fortune Bay (Table 10) was based on approximate historical catch levels and was intended to prevent further increases in fishing effort beyond the 1971 level. In 1973, cohort analyses became the main method of stock assessment and $F_{0.1}$ (Gulland and Boerema 1973) became the main management strategy directed towards stock rebuilding. It is evident, however, from data already presented (Table 8) that the stock continued its precipitous decline throughout the 1970's, due mainly to a combination of successive weak year-classes and high fishing mortality rates. We shall now examine the adequacy of previous estimates of biomass and recruitment of Fortune Bay herring, and the extent to which these estimates contributed to the high fishing mortality rates during the 1970's.

An examination of Tables 11 and 12 indicates that biomass and recruitment levels of Fortune Bay herring were substantially overestimated by cohort analyses until the late 1970's when purse-seine CPUE data no longer were used as the main basis for fine-tuning population estimates. A more detailed examination of the purse-seine CPUE data is therefore in order.

The purse-seine catch rate index (Table 3) used as a measure

TABLE 5. Monthly catch rates (t/landing) of gillnet fisheries for herring in Fortune Bay (C = catch, L = number of landings).

	Monthly catch (t) and catch rate									
	April			May			June			Mean
Year	C	L	C/L	C	L	C/L	C	L	C/L	C/L (t)
1978	0.57	4	0.14	0.58	1	0.58	4.03	1	4.03	0.86
1979	0.79	4	0.20	11.63	48	0.24	4.61	8	0.58	0.28
1980	1.89	12	0.16	10.30	45	0.23	2.87	21	0.14	0.19

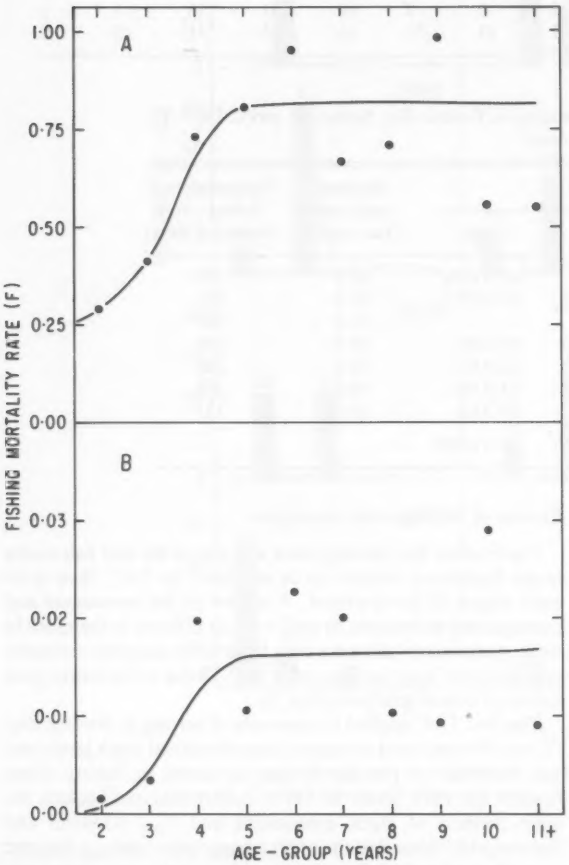

FIG. 3. Relationship between fishing mortality and age-group (i.e. partial recruitment) for the (A) purse-seine fleet and (B) bar-seine fleet as calculated from trial runs of cohort analyses for the years 1971–72.

TABLE 6. Estimation of the 1980 partial recruitment values used as input into cohort analyses.

	Partial recruitment rate			
Age	Purse seine	Bar seine	Gill net	Weighted average
2	0.35	0.10	—	0.13
3	0.50	0.35	0.85	0.48
4	0.90	0.70	0.93	0.79
5	1.00	1.00	1.00	1.00
6	1.00	1.00	0.95	0.99
7	1.00	1.00	0.89	0.98
8	1.00	1.00	0.83	0.97
9	1.00	1.00	0.77	0.95
10	1.00	1.00	0.71	0.94
11	1.00	1.00	0.59	0.92

TABLE 7. Calculation of total instantaneous mortality rates (Z) of Fortune Bay herring by the method of Paloheimo (1961).

	Catch rate (nos./landing)				
Year	4+	5+	6+	Z_{4+}	Z_{5+}
1978	3.34	1.01	0.96	1.22	2.42
1979	1.03	0.99	0.09	0.52	0.53
1980	0.61	0.60	0.58		

of stock abundance was based on operating days as a measure of both searching and fishing effort. An examination of the temporal trend in the catchability coefficient (q = catch rate/exploitable biomass) (Fig. 6A) indicates that q increased substantially between 1967 and 1973 and particularly from 1970 to 1973 when stock abundance began its precipitous decline. The increase in q from 1967 to 1968 occurred when stock abundance was stable (Table 8) and probably reflected fleet learning in similar fashion as observed in the southwest Newfoundland herring fishery for the same fleet (Winters and Hodder 1975). Over the entire period, however, the catchability coefficient was inversely correlated with stock abundance (Fig. 6B). This change in q undoubtedly contributed to the overestimation of stock abundance during the period of stock decline in the early 1970's.

An additional source of error in the estimates of stock abundance in the 1970's was the estimated strength of recruiting year-classes, particularly for the 1970–74 year-classes, which were substantially overestimated (Table 12) for ages 2, 3, and 4. These biasses in recruitment levels were due to the underestimation of partial recruitment rates (PR) (Table 13) and illustrate in striking fashion the likelihood of overestimating a dominant incoming year-class in a depleted herring stock when the PR values are derived from the relative fishing mortality rates as described by the historical F-matrix of cohort analyses. Since the selectivity rate of a purse-seine fishery is likely to increase in the younger age-groups as stock abundance declines, it is desirable to estimate PR values from relative F-value in the most recent years of cohort analyses. However, it is precisely those years that are most unreliable, since they are largely a

TABLE 8. Population matrix of Fortune Bay herring (spring spawners) as derived from cohort analyses for the period 1966–80.

	Population size ($\times 10^{-6}$) at beginning of year														
Age	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
2	3.2	5.4	131.1	29.5	145.0	1.6	5.4	6.3	6.3	0.3	28.4	1.1	0.1	0.2	1.5
3	216.0	2.6	4.4	101.4	23.7	80.3	1.1	3.0	3.1	4.8	0.3	23.1	0.8	0.1	0.2
4	2.2	176.6	2.1	3.5	72.2	12.1	44.0	0.7	1.6	1.3	3.7	0.2	17.0	0.7	0.1
5	2.1	1.8	122.2	1.4	2.8	49.7	4.2	17.9	0.5	0.8	0.6	2.7	0.1	11.5	0.4
6	5.6	1.7	1.4	56.1	1.0	2.2	18.6	0.8	9.5	0.3	0.6	0.3	1.9	0.1	5.9
7	7.3	4.5	1.3	1.0	34.1	0.6	0.7	5.4	0.3	3.7	0.2	0.4	0.1	1.4	0.1
8	4.8	5.9	3.3	1.0	0.6	21.2	0.3	0.2	0.1	1.3	0.1	1.1	0.1	0.1	0.1
9	3.2	3.8	4.4	2.1	0.6	0.3	9.0	0.2	0.1	1.3	0.1	1.1	0.1	0.1	0.1
10	0.1	2.6	2.7	2.9	1.1	0.4	0.1	2.4	0.1	0.1	0.9	0.1	0.7	0.1	0.1
11+	1.2	1.0	2.4	2.5	1.2	1.4	1.0	1.5	0.4	0.9	0.6	0.9	0.5	0.5	0.2
2+ biomass (10^3 t)	38.0	44.0	44.9	36.0	41.1	34.3	19.6	8.4	5.7	3.3	4.3	5.0	4.8	3.6	2.3
5+ biomass (10^3 t)	7.5	6.9	34.7	19.3	12.8	20.7	10.0	7.4	4.4	2.3	1.5	1.7	1.2	3.4	2.2
Catch (t)	193	5668	14 727	6866	9388	15 004	10 570	3254	2268	909	462	579	1000	1192	446

TABLE 9. Fishing mortality matrix of Fortune Bay herring as derived from cohort analysis for the period 1966–80.

	Fishing mortality														
Age	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
2	0.01	0.01	0.06	0.02	0.39	0.13	0.38	0.50	0.07	0.01	0.01	0.03	0.04	0.01	0.03
3	0.01	0.04	0.03	0.14	0.47	0.40	0.29	0.41	0.64	0.07	0.06	0.11	0.06	0.05	0.11
4	0.01	0.17	0.19	0.03	0.17	0.85	0.70	0.11	0.46	0.65	0.10	0.14	0.19	0.38	0.18
5	0.01	0.03	0.58	0.16	0.04	0.78	1.46	0.43	0.31	0.16	0.58	0.14	0.64	0.46	0.23
6	0.02	0.03	0.18	0.30	0.24	0.93	1.04	0.97	0.75	0.38	0.27	1.21	0.15	0.31	0.23
7	0.01	0.11	0.11	0.24	0.27	0.43	0.81	0.45	0.72	0.59	0.07	0.08	1.44	0.14	0.22
8	0.02	0.09	0.23	0.34	0.54	0.67	0.45	0.41	0.58	0.19	0.25	0.46	0.81	0.59	0.22
9	0.01	0.16	0.21	0.44	0.03	0.67	1.10	0.38	0.07	0.13	0.87	0.22	1.91	0.30	0.22
10	0.02	0.17	0.48	1.30	0.26	0.46	0.36	0.44	0.26	0.26	0.25	0.21	0.73	0.15	0.21
11+	0.02	0.16	0.48	1.31	0.27	0.53	0.55	0.47	0.25	0.24	0.22	0.20	0.70	0.40	0.21
Mean F_{5+}	0.02	0.11	0.54	0.35	0.25	0.74	1.06	0.45	0.63	0.37	0.29	0.22	0.40	0.42	0.23

function of the input parameters in the terminal year. Empirical estimates of partial recruitment rates are not subject to such biasses and are therefore more likely to result in unbiased estimates of recruitment.

Factors Affecting Recruitment Variability

An essential ingredient of fisheries management (and particularly for pelagic stocks) is the regulation of the spawning stock size either to maximize recruitment or (as is usually the case) to prevent stock attrition to the level of impaired recruitment. Since this implies a stock–recruit interaction, we shall now examine the impact of density-dependent and environmental factors on recent variations in recruitment levels of Fortune Bay herring.

Estimates of recruitment (at age-group 2) are available for the 1964–75 year-classes from cohort analyses (Table 8). Recruitment estimates for the 1963 year-class were back-calculated from the 1966 population matrix, assuming $M = 0.20$ (catches were negligible during the period 1962–65). These recruitment data were transformed to natural logarithms, since herring recruitment follows a lognormal pattern (Hennemuth et al. 1980). Egg production for the years 1963–65 was obtained from midyear age-specific population numbers as derived from back-calculation of the 1966 population matrix, assuming $M = 0.20$. Temperature and salinity data were summed for the period 6 mo prior to spawning (November–April) (T_1 and S_1) and 6 mo following spawning (May–October) (T_2 and S_2), since these periods were considered to have a broad biological basis. Winter water temperatures have been shown to affect the year-class success of spring-spawning herring in the Baltic (Rannak 1971) as well as controlling the development and spawning time of zooplankton (Mankowski 1966) whose reproductive products form a predominant component of the diet of herring larvae (Bainbridge and Forsyth 1971). Salinity and temperature conditions during and immediately after spawning have been shown by a variety of authors to affect both hatching success and survival of herring larvae (Taylor 1971; Holliday and Blaxter 1960).

Correlation coefficients for the above variables are shown in Table 14. The results indicate that recruitment of Fortune Bay herring was significantly correlated with prespawning temperatures (T_1) but was not correlated with either postspawning environmental conditions or egg production.

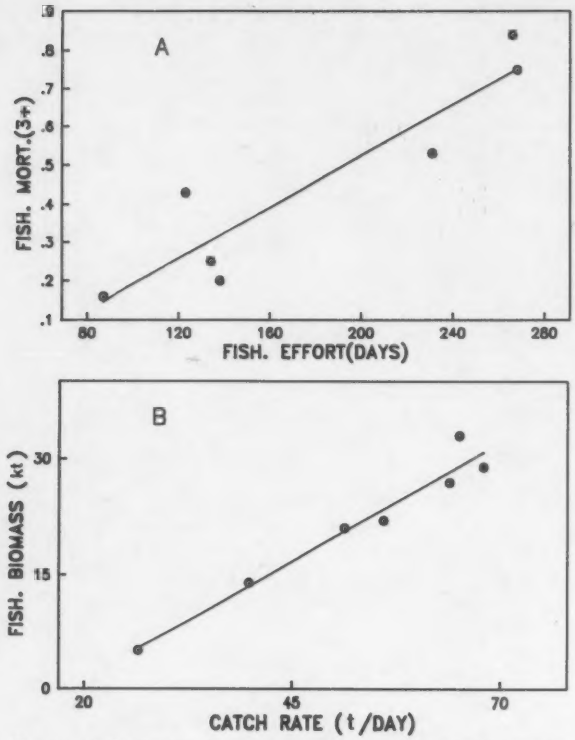

FIG. 4. Relationship between (A) fishing mortality and standardized effort and (B) exploitable biomass and standardized catch-rates of the purse-seine fleet for the period 1967–73.

From these results we have concluded that spawning stock size, i.e. egg production, has had no measurable impact on the recruitment of Fortune Bay herring over the range of stock sizes that have been associated with this population since the early 1960's.

Estimation of Yields under Various Fishing Strategies

It has already been pointed out that the purse-seine fishery that developed in Fortune Bay during the late 1960's was essentially conducted according to a fishing pattern in which strong year-classes were fished very heavily as soon as they recruited to the stock. Since recruitment during the period was apparently unrelated to variations in parent stock size, we shall now assess potential yields from this stock according to the alternative fishing strategies of (*i*) surplus yield removals and (*ii*) $F_{0.1}$ (Gulland and Boerema 1973) fishing mortality. In each case the simulations are initiated with the 1967 age-specific population matrix (Table 8), assuming $M = 0.20$. The estimated $F_{0.1}$ fishing mortality rate (0.29) was derived using the average partial recruitment pattern for this stock as provided in the F-matrix (extended to age 15) for the period 1967–78, and using mean weight-at-age for the same period. Surplus production (SP) is defined as

$$SP = B_{t+1} - B_t$$

where B_t is the 2+ biomass in year t and B_{t+1} is the 2+ biomass the next year. Age-specific removals were then derived assuming the same pattern of fishing mortality as described by cohort analysis for each year.

The results (Fig. 7) indicate that the greatest variability in yields would have resulted from a surplus production pattern of fishing whereas the $F_{0.1}$ strategy would substantially ameliorate

TABLE 10. Description of assessment methods used to provide advice on catch levels for Fortune Bay herring (for TAC's see Table 1).

Terminal year (T)	Method of assessment	Method of F_T estimation	CPUE used	F_T estimate used	Best estimate of F_T	PR method[b]	Recommended fishing level
1972	Historical catch level	—	—	—	—	—	Mean historical effort
1973	Cohort analyses	F versus effort	Purse seine[c]	0.10	0.45	F-mat	$F_{0.1}$
1974	Cohort analyses	F versus effort	Purse seine	0.20	0.63	F-mat	$F_{0.1}$
1975	Cohort analyses	CPUE versus biomass	Purse seine	0.09	0.38	F-mat	$F_{0.1}$
1976	Cohort analyses	Projection from 1975	Purse seine	0.03	0.29	—	$F_{0.1}$
1977	Cohort analyses	F versus effort	Purse seine	0.10	0.22	—	$<F_{0.1}$
1978	Cohort analyses	Projection from 1977	Purse seine	0.15	0.42	—	$<F_{0.1}$
1979	Cohort analyses	Estimation of dominant Y/C from comparisons with adjacent stocks; other year-classes estimated from implied F_T and PR	—	0.40	0.42	Empir.	Lowest practical level
1980	Cohort analyses	Empirical estimate of Z by method of Paloheimo (1961)	Gill net	0.23	0.23	Empir.	Lowest practical level

[a]From 1980 cohort run and considering convergence of F.
[b]See legend to Table 13.
[c]1967–73 time series.

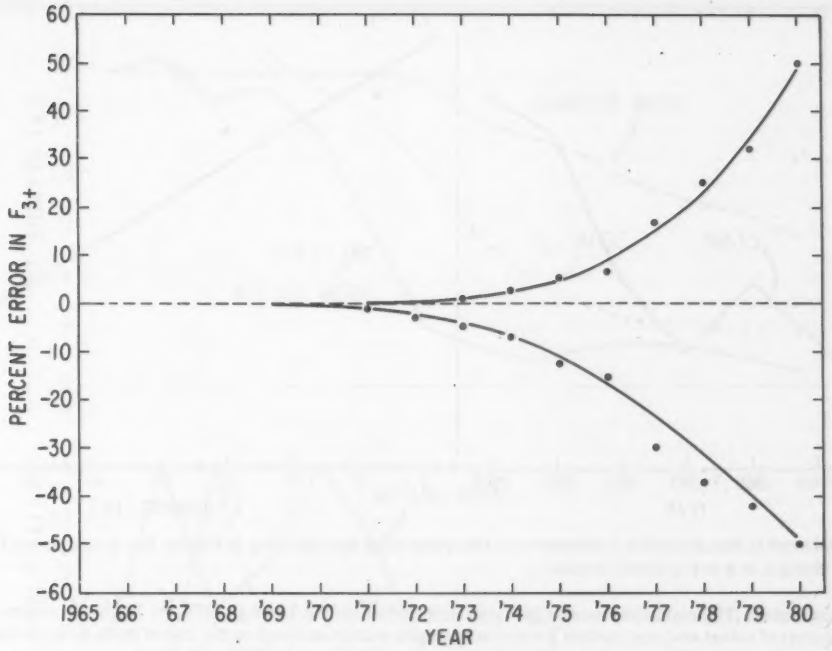

FIG. 5. Sensitivity of cohort analysis of Fortune Bay herring in relation to 50% errors in terminal F (F_T).

TABLE 11. Biomass estimates (2+) ($\times 10^{-3}$) of Fortune Bay herring as estimated in annual assessments for terminal years 1973–80.

Fishery year	2+ biomass estimated from terminal year							
	1973	1974	1975	1976	1977	1978	1979	1980
1980								2
1979							4	4
1978						8	5	5
1977					10	8	5	5
1976				16	8	8	4	4
1975			15	17	5	6	3	3
1974		22	17	17	8	9	6	6
1973	25	22	20	20	11	12	8	8
1972	30		28	28	22	23	20	20
1971	45		43	43	37	38	35	34
1970	53		48	48	43	44	41	41
1969	50		40	40	38	38	36	36
1968	57		49	49	46	46	45	45
1967	53		47	47	45	45	44	44
1966	—		41	41	39	39	38	38

annual variability on yields. This would have occurred at some cost in terms of yield, since the mean annual yield under the $F_{0.1}$ strategy (4600 t) would have been somewhat lower than the historical pulse-fishing yield (5200 t/yr) but considerably higher than the mean annual yield from the surplus production mode (2250 t/yr). The surplus production strategy however would not have prevented the decline in stock abundance but would have reduced the rate of decline; however, if maximizing population stability and mean age were to be the main objectives of management strategy then obviously the surplus production pattern of fishing would be most desirable.

TABLE 12. Estimates of recruitment (in millions of fish at age-group 2) of the 1969–78 year-classes as derived from age-groups 2–4 from annual assessments of Fortune Bay herring.

Year-class	Recruitment estimation from terminal year							
	1973	1974	1975	1976	1977	1978	1979	1980
1978								(2)
1977							<1	<1
1976						<1	<1	<1
1975					7	1	1	1
1974				10	44	38		28
1973			10	10	1			<1
1972		—	19	10				6
1971	85	40	29					6
1970	22	15						5
1969	2							2

Discussion and Conclusions

The analyses presented in this paper have shown that the recruitment variability exhibited by Fortune Bay herring was more strongly associated with environmental factors than with population fecundity. We do not wish to rationalize our choice of environmental signals, since plausible rationales could be provided for a wide variety of permutations of salinity and temperature. Furthermore, Saville (1959) and Gulland (1965) pointed out rather well the pitfalls of retrospective correlations between fish production and environmental factors. However, it is the general environmental control of herring recruitment that is the important conclusion, and this is supported by the pattern of year-class strength in adjacent herring stocks. When a large

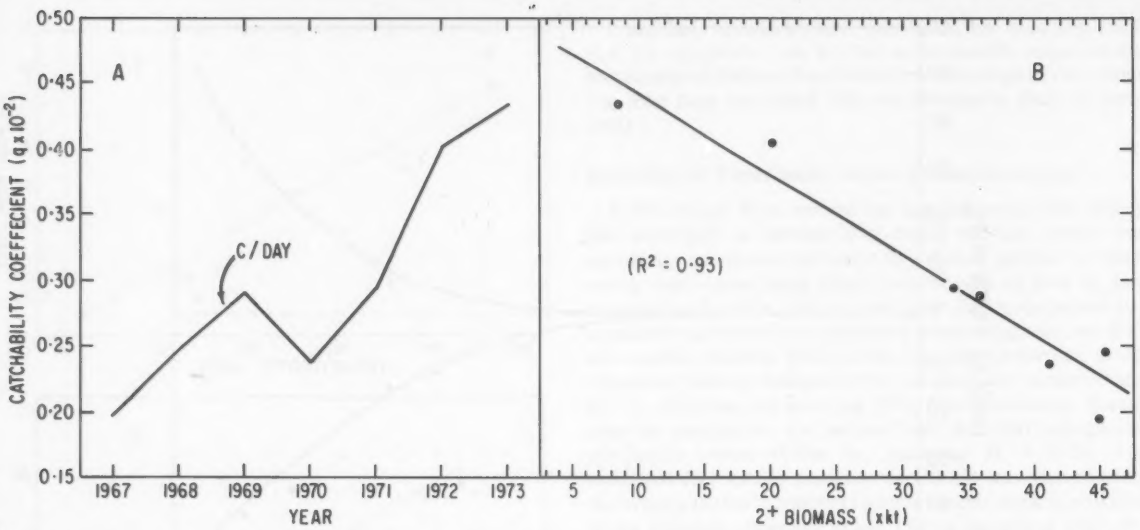

FIG. 6. (A) Temporal trend in the catchability coefficient (q) of the purse-seine fleet operating in Fortune Bay for the period 1967–73 and (B) the relationships of such changes in q to population biomass.

TABLE 13. Partial recruitment (PR) multipliers used in the assessment of Fortune Bay herring, 1973–79. Method A refers to relative F-values from the historical F-matrix of cohort analyses; method B refers to an empirical estimate based on the ratio of catch-at-age to the purse-seine catch-at age. The best estimate refers to the PR estimate from the relative age-specific F's in the 1980 cohort run.

	1973		1974		1975		1976		1977		1978		1979	
Age	PR used	Best est.	PR used	Best est.	PR used	Best est.	PR used	Best est.	PR used	Best est.	PR used	Best est.	PR used	Best est.
2	0.25	1.00	0.05	0.11	0.05	0.03	(0.10)	0.02	0.05	0.14	0.05	0.10	0.05	0.02
3	0.60	0.90	0.30	1.00	0.25	0.18	—	0.21	0.50	0.50	0.50	0.14	0.50	0.12
4	0.80	0.25	0.45	0.73	0.50	1.00	—	0.35	0.80	0.64	0.80	0.24	0.80	0.91
5	1.00	1.00	1.00	1.00	1.00	1.00	—	1.00	1.00	1.00	1.00	1.00	1.00	1.00
PR method	A		A		A		A		A		A		B	

year-class occurs in one stock the same year-class appears strong over a fairly large spatial scale. The 1968 year-class of spring spawners that was strong in Fortune Bay was also strong in the Southern Gulf of St. Lawrence herring stocks (Winters et al. 1977) and in herring stocks along the northeast coast of Newfoundland (Wheeler and Winters 1982). The 1974 year-class was moderately strong in Fortune Bay, on Newfoundland's west coast (Moores et al. 1981), the Southern Gulf (Winters and Moores 1980), and, although not a substantial year-class, the strongest for several years on Newfoundland's northeast coast (Wheeler and Winters 1982). This parallelism in year-class strength lends credence to the concept that herring recruitment is controlled mainly by environmental factors rather than spawning stock size. Hourston (1980), Taylor (1963), and Stevenson (1962) arrived at the same conclusion for Pacific herring. Cushing and Dickson (1976) cited numerous examples of correlations between fish production and environmental factors and pointed out that climatic changes are pervasive and worldwide and events in one region can quite properly be correlated with those in another. This would be even more applicable on a spatial scale the size of the distribution area of the abovementioned herring stocks. Cushing and Dickson (1976) continued by stating that the only way climatic events can be connected causally with events in fish populations is by means of a structure such as the match–mismatch hypothesis. This states that the amount of food available depends upon variability in the production cycle, one critical determining factor of which is temperature. When there is a good match between larval production and the food production cycle which is determined by environmental factors that are inherent over a

TABLE 14. Simple correlation coefficient between herring recruitment and various environmental and population parameters for the year-classes 1963–75 (R = log recruitment, E = population fecundity, T_1 = sum of mean monthly temperatures from November to April, T_2 = sum of mean monthly temperature from May to October, S_1 = sum of mean monthly salinities from November to April, and S_2 = sum of mean monthly salinities from May to October).

	Correlation coefficient				
Dependent variable	E	T_1	T_2	S_1	S_2
R	0.35	0.60[a]	0.01	0.29	0.33

[a] $p < 0.05$.

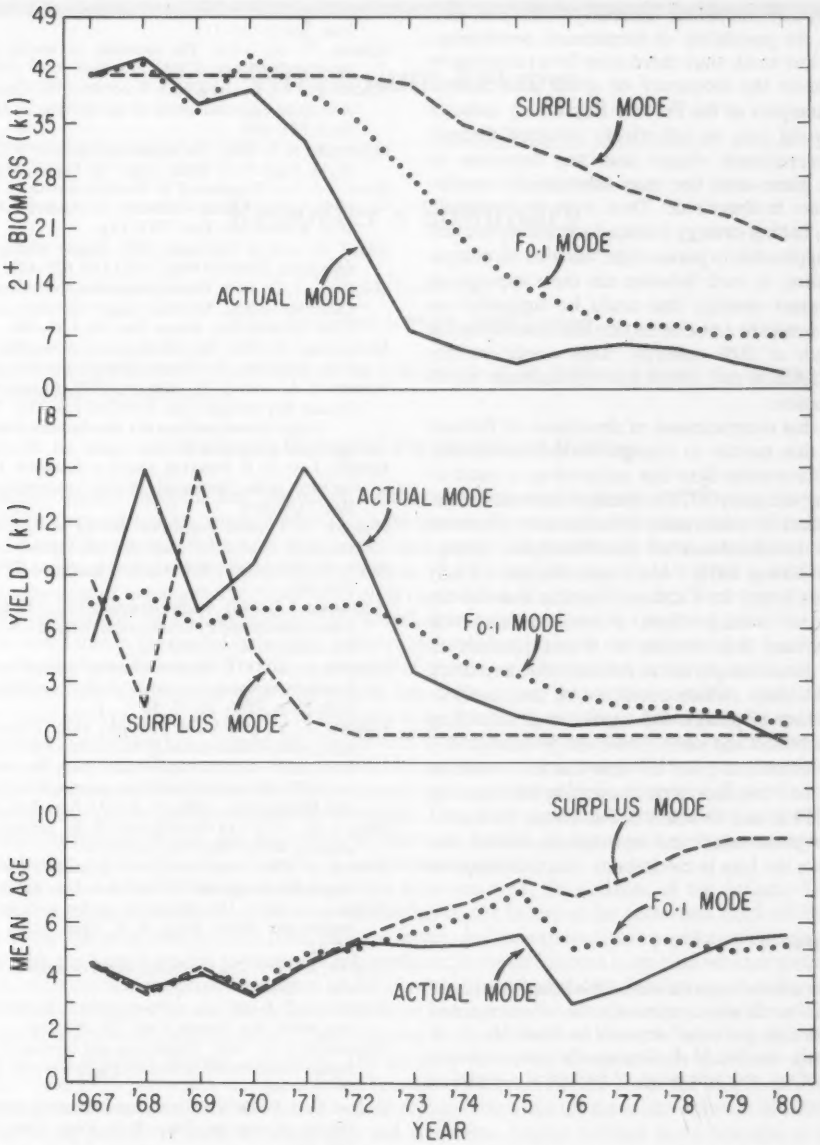

FIG. 7. Temporal trend in biomass, yield, and mean age of Fortune Bay herring according to different fishing strategies.

large spatial scale, one may expect a high larval survival and good year-classes over the same scale. This match–mismatch theory was disputed by Iles and Sinclair (1982) who proposed that year-class size in herring is related to the size of the larval retention area, annual variations of which are determined by various oceanographic parameters rather than spawning stock size.

Management objectives for the utilization of pelagic fish stocks often imply a strong biological basis as the rationale for yield regulation. These objectives are generally expressed in terms of protection of the spawning stock and/or rebuilding biomass levels through moderation of the fishing effort, often at or below the $F_{0.1}$ level. In both cases it is assumed that reduced fishing mortality rates will assure biomass enhancement and prevent recruitment attrition. The analyses presented in this paper, however, demonstrate that factors other than fishing mortality and parent stock size may produce substantial changes in population abundance. Annual production, both in the form of new recruitment or somatic growth (Moores and Winters 1982), has been shown to be mainly controlled by environmental rather than logistic factors.

Thus, given the exaggerated recruitment variability of most pelagic fish stocks (and particularly those in the extremes of their range, as are Newfoundland herring stocks), stock rebuilding through protection of the spawning stock cannot be assured but will instead be determined mainly by recruitment

changes induced by environmental variability. This does not, however, rule out the possibility of recruitment overfishing, since at extremely low stock sizes there must be a reduction in year-class size and/or the frequency of good year-classes. Furthermore, the analyses of the Fortune Bay fishery indicate that the greatest yield may be effectively obtained through pulse-fishing of recruitment surges and that increases in catchability by the purse-seine fleet may substantially ameliorate dramatic declines in abundance. Thus, even the economic rationale of the $F_{0.1}$ fishing strategy (reduced variability in catch rates) may not be applicable to purse-seine fisheries on pelagic fish stocks. Therefore, in such fisheries the most appropriate long-term management strategy that could be supported on biological grounds would be a minimum size limit established at or above the length of 50% maturity. This would prevent spawning stock extinction and would also approximate yield-per-recruit optimization.

We have shown that overestimates of abundance of Fortune Bay herring were due mainly to changes in the catchability coefficient of the purse-seine fleet that occurred as a result of stock decline during the early 1970's. Similar increases in the catchability coefficient of purse-seine fisheries were observed during the decline in abundance of the Norwegian spring-spawning herring (Ulltang 1978). Also, both Murphy (1966) and MacCall (1976) found for California sardine that for the available measures of fishing effort, q increased as stock decreased. For Fortune Bay herring it is not possible to determine whether these changes in catchability were a result of changes in fleet efficiency (which could not be measured) or inherent characteristics of pelagic fish stocks (e.g. schooling behaviour and distribution and size). However, Powles (1981) has shown from a theoretical point of view that in a situation where density remains constant with decreasing biomass the relation between CPUE and biomass is not linear. In such a case, no matter how purse-seine catch rate data are treated, one is unlikely to remove the bias in catchability due to changes in stock size.

Acknowledgments

The authors wish to acknowledge the staff of the Pelagic Section of the Fisheries Research Branch who contributed to the collection of data used in this document. In particular we wish to thank Mr. C. I. Barbour, Mr. R. Chaulk, and Mr. M. F. Dawson who were intimately involved in the collection and processing of biological samples of herring.

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Symposium Review

Reporter's Summary

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The following summary is a synopsis of my impressions of the papers presented and my conclusions drawn from the symposium.

Session 1: Biological Perspectives of Herring

Whitehead[1] quoted Lacépède that "the use of herring defined the wealth of nations." Herring, however, is only 1 of 326 clupeoid species, most of which have the remarkable acoustico-lateralis receiver (described by Blaxter), a device to detect objects at short angles and ranges independent of depth, useful in schooling species. The annual world catch of clupeoids amount to 14.5 million tons, mostly in tropical and subtropical seas. Management of herring stocks based on a great expenditure of research has not been very successful. What is the prospect for the management of tropical and subtropical species with very much less information?

Blaxter noted that in the early 1960s, the catches of Atlantic herring each year amounted to 4 million tons before collapse. Svetovidov (1952) distinguished five groups of herring, but common to all are certain characteristics: they lay demersal eggs which hatch into large larvae, they school as adults, and manifest a complex racial system. They are flexible in response to environment, evincing a broad range of spawning in latitude which is expressed in considerable differences in racial characters. The physiological nature of the herring not only includes the acoustico-lateralis detector, but also a visual acuity of 10′ of arc, a low frequency sensitivity of herring of 100 Hz, and the rapid response by the Mauthner cells. Recently, Blaxter has shown with infrared instruments that herring filter-feed at night. They show great flexibility in vertical migration. The stocks vary enormously in size, can colonize new areas very readily, and can recover from very low levels. Yet because they school they are vulnerable to recruitment overfishing.

Lasker surveyed some of the great changes that have occurred, the collapse of the Atlanto–Scandian herring, the exchange of sardine and anchovy off California, the failure of the anchoveta stock off Peru, the recovery of the Japanese sardine stock from very low levels, and the extraordinary population changes shown by scales from the Santa Catalina sediments. Lasker referred to the differences in opinion whether predation or starvation of larvae was the proximate cause of differences in larval mortality. Northern anchovies consume up to 100 anchovy eggs·d^{-1}, and many larvae are eaten by euphausids. *Aurelia* may control the numbers of herring larvae under some circumstances. Lasker showed that jack mackerel larvae 3.5 mm in length may lose 57–70%·d^{-1} in numbers through starvation. The anchovy larvae eat *Gymnodinium splendens* more than 20–40·L^{-1}; the 1975 year-class may have failed because *Gonyaulax polyedra* was the only food available. From the sedimented scales, MacCall (quoted by Lasker) has shown that the cumulative growth of sardine was depressed during periods of anchovy abundance and vice versa. Lasker referred to the attempts to explain recruitment to the manhaden and Pacific mackerel stocks by multiple regression analysis with environmental factors. He concluded that "everything limits recruitment, but some things more than others."

Session 2: Spawning, Development, and Survival of Early Life Stages of Herring

Haegele and Schweigert displayed charts of Atlantic and Pacific herring spawning grounds and time-plots of spawning seasons. Larvae tend to be retained near the spawning grounds. Autumn Atlantic deepwater spawners lay their eggs in up to 40 m depth in one or two layers, where currents can reach 1.5 knots and where temperature and salinity are relatively high. The shallow-water spawners (Pacific and spring Atlantic herring) lay their eggs on vegetation up to 15 m in depth in bays and inlets at 6.5–10.0°C and in salinities of 22–29‰. The vegetation may supply oxygen to the eggs.

Alderdice and Hourston examined the survival of eggs and larvae in response to environmental factors. There are optimal responses common to the factors of temperature and salinity. The efficiency of oxygen

[1]Reference to authors without dates applies to those presenting papers published in this issue.

supply to the eggs depends on the colloidal osmotic pressure gradient across the membrane, on the sinking of deoxygenated water, on convection within the egg masses, and upon wave surge. Egg survival also depends upon packing density, whether regular or not, and upon the nature of the substrate. Between 10 and 21‰ there is little larval mortality in experimental determinations, but it increases with higher salinity. The salinity range in the Strait of Georgia is 27.3–28.6‰ and the lethal range is 27.5–31.7‰. However, larval surveys showed a 70% loss rate per week offshore and 78% inshore and so the salinity was not effectively lethal. The guts of the larvae were 42% full, so the loss was probably due to predation. The great geographical range of the herring, particularly in the Pacific, may be explained to some degree by salinity tolerance. At very low temperatures when salinity is also low in high latitudes, the species survives well. In temperate waters they appear to live in the region of optimal response.

On the question of year-class strength and survival of 0-group clupeoids, Smith suggested that both the effects of stock and of environmental factors are too weak for the predictive purposes of management. For the northern anchovy, he proposed six factors of importance: (a) a stable and stratified ocean for spawning and larval feeding, (b) a temperature of at least 15°C to accelerate hatching and first feeding, (c) the days should lengthen because the animals are visual feeders, (d) moderate upwelling, (e) strong upwelling for the juveniles that feed on diatoms, and (f) a large adult population so that some spawning can occur before the spring bloom. He described the mortality rate of a cohort with respect to the creation of biomass. He noted that differences in the period of cumulated mortality might be more important than differences in the instantaneous rate. Early larval mortality rate amounts to about 0.2, and at the onset of schooling it is reduced to 0.1. Of competitive mechanisms, Smith suggested that space, food, cannibalism, or predation may be important. Food must be of little importance because the growth rate of survivors matches the maximal growth rate observed in the laboratory. Cannibalism appears to be a low and constant source of mortality. Predation is of importance because off Peru the bird population sometimes increases with high anchoveta recruitment.

Aneer showed that the mortality of Baltic herring eggs was greater on filamentous algae, the quantity of which has increased during the seventies.

Session 3: Age, Growth, and Reproductive Characteristics of Herring

Kerr and Dickie worked on the 0-group cohorts in St. George's Bay. They used a mass balance equation to derive a "realized metabolic scope" as a proportion of the total scope. This ratio differed between cohorts, and the earliest was less successful than the last.

Hay presented a paper on the reproductive biology of the Pacific herring. The gonadosomatic index peaks in March, in males somewhat earlier than in females. A maturation index was developed based on the ratio of oocyte diameters to those of resting oocytes. Fecundity tends to be high in the south and low in the north. Remarkable pictures were shown of the spawning in the Strait of Georgia; the locations tend to be the same from year to year. A clear relationship was established between time of spawning and temperature. The fish appear to spawn in waves about 14 d apart, and those farther north spawn later.

Ware examined surplus energy, the sum of energy devoted to growth and reproduction. Between 1946 and 1962, the mean weight-at-age of 6-yr-old fish increased by a factor of 1.7 (northern British Columbia stock). He found that the reproductive value (number of offspring-at-age potentially produced during the rest of the lifetime) peaked at an age of about 9 or 10. The size factor in density-dependent growth was plotted on exploitation rate, and with $M = 0.45$ the observed factor of 1.5–1.7 was expected at $E = 0.3$. Then the stock is as resilient as the virgin stock, i.e. recruitment was not impaired.

Haist and Stocker investigated juvenile growth rate, adult surplus energy, and the maturation schedule for the Strait of Georgia herring stocks. They plotted surplus energy against adult biomass and fitted a multiple exponential regression, which suggested a dome, maximal at about 120 000 tonnes.

Session 4: Clupeid Production and Recruitment Models

In the menhaden stocks, north and south of Cape Charles, density-dependent growth probably occurs before recruitment (Reish et al.). Natural mortality was estimated by a cohort analysis from tagging experiments. Migration probabilities were estimated from differences in catches per effort corrected for effort changes. Fishing mortality was estimated from cohort analysis. The stock–recruitment relationship was shown corrected from Ekman transport.

Anthony and Fogarty compared catches of Gulf of Maine herring with temperature. In the stock–recruitment relationship, recruitments were separated into high and low temperature components. However, a more detailed analysis showed that high recruitment occurred in the cold winters; between 1955 and 1967, growth rate was dominated by abundance, but when the stock was reduced after 1968, temperature became the dominant factor. There is thus a conflict between the detailed analysis from 1955 onward and the more general one in the stock–recruitment relationship. In the latter, differences in temperature might have indicated a more general change in climate.

Stocker et al. constructed a stock–recruitment model from an age-structured reconstruction of catches in

numbers. There was a fourfold variation in recruitment between 1951 and 1980, and no time trend in the residuals. Four environmental relationships were evaluated. Significant relationships were found with mean April–July sea surface temperatures and mean June–July Fraser river discharge. A dome was generated with an additional squared sea surface temperature term. A new stock reconstruction showed some improvement with the environmental factors added.

In the Bering Sea, Fried and Wespestad described a model of the stocks. Two growth curves were used for six spawning groups. Natural mortality was estimated from catch curves. A maturity ogive curve was used. An exploitation rate of 0.2 was recommended because $E_{MSY} = 0.3$ (from a yield-per-recruit curve). Spawning stock biomass was estimated from aerial surveys.

Burd described events in the recovery of the Downs and Dogger stocks in the North Sea. He showed that individuals of the two groups could be separated using mean egg weight plotted against fecundity per $(\text{length})^3$. Recruitment to the two stocks (recovered in different year-classes) and meristic characters remained the same, so the stocks appear to be distinct. Burd also showed that the 3-yr-old recruits returned to a spawning ground at the same location in three years. It is well known that differences in larval abundance indicate differences in stock size. Recruitment to the Downs stock can now be forecast from 0-groups on arrival on the beaches in July, 6 or 7 mo after hatching (Wood 1983). Hence, the crucial processes in the determination of recruitment occur before arrival on the beaches, as is also true for the southern North Sea plaice (Rauck and Zijlstra 1978). Growth in the two stocks is density dependent (on stock size at 1 yr old), a difference of about 40% in weight occurring for a difference of 15 times in stock.

Session 5: Biological, Social, and Economic aspects of Herring Fisheries Management

The state of management in the Northeast Atlantic was described by Jakobsson. He contrasted the rapid collapse of the Atlanto–Scandian stock with the slow and successive decline of the North Sea stocks. In the Atlanto–Scandian stock, the stability secured by the survival of moderate year-classes was destroyed when such year-classes were obliterated by the fishery for immature herring; further, catchability increased by a factor of 3 in the last years of the fishery. The slow decline in the North Sea as the fishery shifted from stock to stock has been followed by recovery after a ban; that recovery is monitored by larval survey and with acoustic methods. However, despite the return of year-classes as large as those in earlier years, 90% of the catch in numbers comprised immature fish taken illegally. There are two major problems: (a) agreements in the North Sea are not yet enforced and (b) large fleets remain, which await the recovery of the fishery.

Morita described the long decline of the Hokkaido spring herring stock and the sharp collapses of stocks in the Sea of Okhotsk and on either side of the Kamchatka peninsula. He also described the present attempts to recover the Hokkaido stock by the release of artificially reared herring at a length of 6.6 cm.

Exploitation in the eastern Pacific was described by Trumble and Humphreys; the system is based on spawn surveys and hydroacoustic surveys. Age distributions have been more or less ignored, but the need to set quotas before the start of the fishery has led to a demand for reliable estimates of recruitment.

Doubleday examined the vulnerability of herring stocks to failure and pointed out that because the animals did not grow much during their adult lives, the variability of recruitment was not damped as in demersal stocks. He made a model that expressed the effect of variable recruitment on the stocks and concluded that fishing mortality should not exceed 0.2 if recruitment failure was to be avoided. Wilimovsky put in a vigorous plea for the adoption of error estimates in quotas and of risk analysis in stock assessment procedures.

Conclusions

The following conclusions summarize what I learned from the symposium.

Stock Separation

There is a complex racial system based on a set of spawning grounds, each of which is very small and occupied at the same season each year. There are two questions: (a) In the diffusive sea, why do they use such narrow grounds? (b) How do they find their way there? The answer to the first may be in the field of genetics, for if a stock includes a number of spawning groups, the maximal variability of the genotype is obtained. The answer to the second question may be in the field of physical oceanography, how a group of fish may make use of water structure and movement to find where they want to be and how larval patches retain their identity between spawning ground and nursery ground. The physicists are now able and interested to work on such small scales. Individuals of stocks, in the North Sea at least, can now be separated and the recruits to the recovering Dogger stock return to the same narrow grounds for each of three years. The geneticists have not yet been very successful with herring; perhaps they should sample the spawning grounds more precisely.

Conclusion 1

Stocks should be defined more closely and assessment biologists should be less cavalier in their allocation of management units.

Generation of Recruitment

It appears that herring recruitment, like plaice recruitment, at least in the southern North Sea, can be forecast about 6 or 7 mo after hatching and the critical period may extend from the time of first feeding to arrival on the nursery ground. During this period the maximal growth rate of plaice remains high, $0.08 \cdot d^{-1}$; within 3 wk of arrival on the nursery grounds it has dropped by a factor of 4. Hence, the critical period is one of high growth rate and declining mortality rate.

Conclusion 2

If the critical period is that between the time of first feeding and arrival at the nursery, we should consider predation and starvation as equivalent factors, not exclusive ones.

Growth

In a number of studies the presence of density-dependent growth was recorded. Ware found that at an exploitation rate of 0.3 ($M = 0.45$), and a 1.5-fold increase in weight-at-age, the stock would be as resilient as the virgin stock. Within such a system, compensation is generated by density-dependent fecundity.

Conclusion 3

It should be established whether density-dependent growth is a sufficient compensator.

Recruitment

The recruitments to the Gulf of Maine herring stocks were related to temperature both directly and inversely; sea surface temperatures and river discharge were found to be of importance in the Strait of Georgia and in Fortune Bay.

Conclusion 4

The detailed mechanisms concealed in those measurements that happen to be available should be elucidated more fully.

Management

Some assessments are made with catch-at-age models without independent stock estimates, and others are assessed at $E = 0.2$ without any catch-at-age data from which a model supporting that rate might be constructed.

Conclusion 5

Management requires both distributions of catch-at-age and independent estimates of stock, with error analyses.

Herring stocks have collapsed all too readily under the pressure of fishing. This is because the variability of recruitment is not damped in the stock by continued growth of the adults after maturity. Consequently, recruitment overfishing is an innate danger.

Conclusion 6

Herring stocks should be exploited lightly ($F = 0.2$–0.3).

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